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Reconstructing Cetacean Brain Evolution Using Computed Tomography

LORI MARINO,* MARK D. UHEN, NICHOLAS D. PYENSON, AND BRUNO FROHLICH

Until recently, there have been relatively few studies of brain mass and morphology in fossil cetaceans (dolphins, whales, and porpoises) because of difficulty accessing the matrix that fills the endocranial cavity of fossil cetacean skulls. As a result, our knowledge about cetacean brain evolution has been quite limited. By applying the noninvasive technique of computed tomography (CT) to visualize, measure, and reconstruct the endocranial morphology of fossil cetacean skulls, we can gain vastly more information at an unprecedented rate about cetacean brain evolution. Here, we discuss our method and demonstrate it with several examples from our fossil cetacean database. This approach will provide new insights into the little-known evolutionary history of cetacean brain evolution. *Anat Rec (Part B: New Anat)* 272B:107–117, 2003. © 2003 Wiley-Liss, Inc.

KEY WORDS: computed tomography; CT; Cetacea; imaging; fossil; endocranial; brain; evolution; encephalization

INTRODUCTION

The origin and evolutionary history of Cetacea (dolphins, whales, and porpoises) represents one of the most dramatic and provocative transformations in the fossil record. Cetacea consists of one extinct and two modern suborders. The Eocene suborder, Archaeoceti, contained approximately 30 (described) genera (updated from Thewissen, 1998) and survived from the early Eocene, around 53 million years ago (Ma) until the late Eocene, around 38 Ma (Barnes et al., 1985; Bajpai and Gingerich, 1998; Uhen, 1998). Of the modern suborders,

Mysticeti (comprising 11 living species of baleen whales) are first found in the fossil record in the latest Eocene (Mitchell, 1989) and Odontoceti (comprising 66 living species of toothed whales, dolphins, and porpoises) are first found in the fossil record in the early Oligocene (Barnes et al., 1985). Cetacean terrestrial ancestry is closely tied to that of ungulates (hooved mammals) and particularly Artiodactyla, the “even-toed” ungulates. For many years, molecular evidence has indicated that cetaceans are embedded in the paraphyletic Artiodactyla and that hip-

popotamids are their extant sister group (Nikaido et al., 1996; Shimamura et al., 1997; Gatesy, 1998; Milinkovitch et al., 1998). Recent fossil morphologic evidence confirms an artiodactyl–cetacean link from both early Eocene protocetid (Gingerich et al., 2001) and pakiicetid (Thewissen et al., 2001) whales (Geisler and Uhen, 2003). See Figure 1 for a phylogenetic tree depicting the ranges and phylogenetic relationships of extinct and extant cetacean families.

Some of the most significant evolutionary changes that occurred among cetaceans are in brain size and structure.

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Integrative Biology and Museum of Paleontology at the University of California, Berkeley, is interested in evolutionary development, paleoecology, and major evolutionary adaptations. Dr. Frohlich is an anthropologist in the Department of Anthropology at the National Museum of Natural History, The Smithsonian Institution. His research includes the studying of mortuary practices in the Middle East and in Alaska, and the application of computed tomography to the study of archaeological artifacts, human remains, and paleobiological specimens.

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Skeletal fossils document the major transformations in cranial and postcranial morphology that occurred throughout cetacean evolution (Gaskin, 1982; Barnes, 1985; Oelschlager, 1990; Buchholtz, 1998; Luo, 1998). In addition, some of the most significant evolutionary changes that occurred among cetaceans are in brain size and structure. Numerous lines of evidence indicate that the terrestrial ancestors of

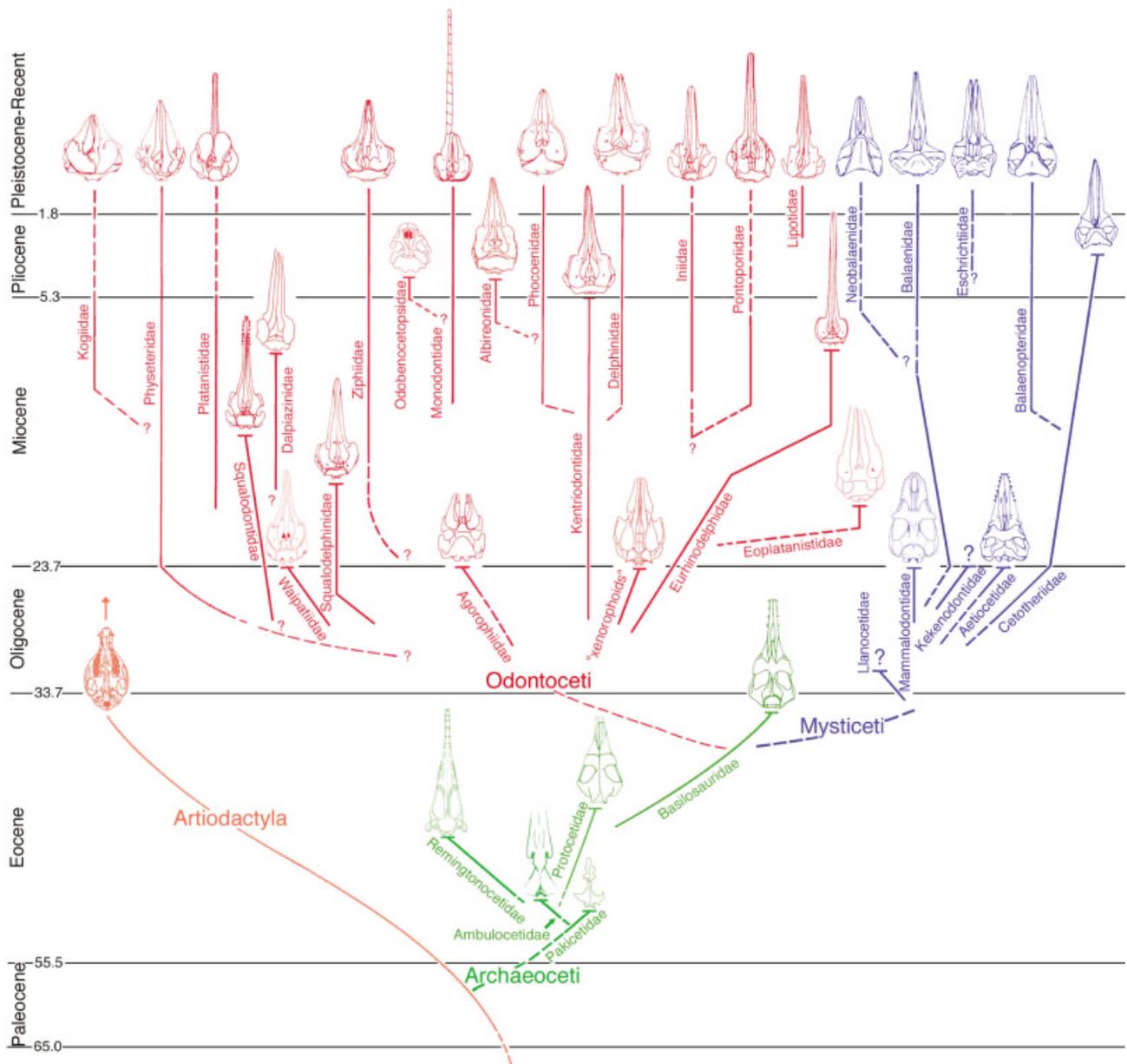


Figure 1. Phylogenetic relationships among families of Cetacea. Families of the paraphyletic suborder Archaeoceti are shown in green, whereas those of Mysticeti are shown in blue, and those of the Odontoceti are shown in red. Ranges of families are shown in solid colored lines, and phylogenetic links are shown in dashed lines. Some families (such as the Basilosauridae) are paraphyletic in that they are thought to be ancestral to other groups of cetaceans (in this case, the Neoceti (Odontoceti+ Mysticeti)). This figure is based on Figure 1 of Barnes et al. (1985).

cetaceans were not particularly highly encephalized and possessed typically organized mammalian brains (Edinger, 1955; Gingerich, 1998). The encephalization quotient (EQ) quantifies the actual brain size of an animal compared to the expected brain size of an animal of that body weight within a given reference group. EQs higher than 1 are greater than expected, and those less than 1 are lower than expected. Presently, when compared to other modern mammals, sev-

eral cetacean groups with EQs in the range of 4.0 to 5.0, possess encephalization levels significantly higher than all other mammals except modern humans with EQs of 7.0 (Marino, 1998) and evince evidence of a substantial degree of morphologic divergence and cortical reorganization resulting in a different elaborative mode from other mammals (Glezer et al., 1988). Therefore, cetacean brains have changed significantly throughout their evolution. A longstanding

problem has been that the data and analysis techniques for determining the pattern of that dramatic change from the terrestrial ancestral form to the present form have not been available.

CETACEAN NEUROANATOMY FROM ENDOCASTS

There have been relatively few estimates of brain mass and/or brain-body mass ratios in fossil cetaceans

because of difficulty accessing the matrix that fills the endocranial cavity of fossil cetacean skulls, which is often very hard and difficult to remove. Also, even when the matrix is removed, it is difficult and time consuming to make accurate artificial endocasts from which volume measurements can be made. Several early estimates of brain mass from endocranial casts have been published (Dart, 1923; Marples, 1949; Breathnach, 1955). More recently, Gingerich (1998) used natural endocasts to reinterpret brain and body mass for several archaeocetes and calculated EQs relative to modern terrestrial mammals ranging from 0.25 to 0.51, demonstrating that early semiaquatic and later fully aquatic archaeocetes possessed levels of encephalization dramatically lower than most modern cetaceans.

In addition to serving as a proxy for brain size, natural endocasts have also served as the basis for morphologic descriptions of brain contours in archaeocetes and early modern cetaceans (Edinger, 1955). Evolutionary changes in brain organization are not as easily assessed as changes in brain size. Often, as in the case of cetaceans, the enlarged cerebrum masks the structures underneath. However, many morphologic and surface features can be evaluated and conservatively interpreted from the contour of fossil endocasts and the endocranial cavity wall. Various morphologic features of fossil cetacean endocasts have been noted in the literature, including cerebral asymmetry (Stefaniak, 1993), lobular morphology (Kellogg, 1936; Edinger, 1955; Czyzewska, 1988; Stefaniak, 1993), the relative size of major structures (Kellogg, 1936; Edinger, 1955; Czyzewska, 1988; Stefaniak, 1993), and imprints of cranial nerves (Kellogg, 1936; Edinger, 1955; Czyzewska, 1988). These kinds of observations, when interpreted cautiously, can serve as the basis for inference about functional changes in the brains of fossil cetaceans.

CETACEAN NEUROANATOMY FROM COMPUTED TOMOGRAPHY

Our understanding of cetacean brain evolution has been hindered by the slow trickle of data that has accumu-

lated over the decades from examinations of either natural or artificial endocasts. In the past few years, computed tomography (CT) imaging has become a breakthrough investigative tool in the study of fossil endocrania because it allows for nondestructive visualization and measurement of endocranial features and digital reconstruction of specimens. CT involves the application of a collimated series of x-rays through the target object to produce a series of sectional images, called tomographs, which reflect the radiographic densities of tissues in the plane of scanning. When radiographic densities in the sediment that fills the endocranial cavity are sufficiently different from that of the surrounding bone, the image presents a way to visually isolate, measure, and reconstruct the endocranial cavity.

In addition to serving as a proxy for brain size, natural endocasts have also served as the basis for morphologic descriptions of brain contours in archaeocetes and early modern cetaceans.

We have used CT to elucidate and measure the endocranial structure of fossil cetacean skulls for the past 5 years. CT has allowed us to gain unprecedented views and insights into the previously largely inaccessible world of fossil cetacean endocranial morphology. The result has been a substantial increase in the slope of our knowledge about cetacean brain evolution. Here, we describe our approach and some of the CT-based methods we are using in the course of our investigations of fossil cetacean endocrania to reconstruct cetacean brain evolution.

OUR PROJECT

Over the course of approximately 13 million years of evolution, from around 52 Ma to around 39 Ma, ceta-

ceans transformed from a terrestrial (Thewissen et al., 2001), to a semiaquatic (Gingerich et al., 2001), to a fully aquatic creature (Uhen, 1998). Previous studies indicate that Eocene cetaceans (archaeocetes) are not particularly encephalized when compared with modern odontocetes (Gingerich, 1998; Marino et al., 2000). Marino et al. (2000) was the first study of cetacean encephalization to use CT methodology to visualize, measure, and reconstruct endocranial features of archaeocete fossils. The value of CT was demonstrated in this study by the fact that we obtained more data on archaeocete brain size by using CT than has been collected from natural and artificial endocasts during the past several decades.

In Marino et al. (2000), we suggested that the principal features of increased encephalization in modern cetaceans emerged as a result of selective pressures that occurred well after the initial transition from a terrestrial to aquatic existence. This assertion was based on our analysis of encephalization patterns showing that there was little change in encephalization over the entire transition in lifestyle from terrestrial to aquatic. This observation suggests that hypotheses about strong drivers of cetacean brain evolution should focus on factors other than the terrestrial-to-aquatic transition.

There is a prodigious body of literature devoted to hypotheses about both the intelligence of cetaceans and the variables that have shaped the evolution of such large brains (Ridgway et al., 1966; Jerison, 1978, 1986; Eisenberg, 1986; Herman, 1986; Worthy and Hickie, 1986; Glezer et al., 1988; Ridgway and Wood, 1988; Marino, 1996; Connor et al., 1998). Theories have highlighted such varied and not altogether independent factors as social ecology (Connor et al., 1998), communication (Jerison, 1986), climate change (Davies, 1963; Whitmore, 1994), echolocation (Jerison, 1978; Wood and Evans, 1980; Worthy and Hickie, 1986; Oelschläger, 1990), and even diving and oxygenation demands as a constraint on brain size (Robin, 1973). The first step in determining which (if any) of these hypotheses are potential explanations for the origin and evolution of large brains in cetaceans, is to identify

TABLE 1. The number of species (and families) for each geologic epoch of the cenozoic era included in this study*

Epoch	Start (Ma)	End (Ma)	Archaeoceti	Mysticeti	Odontoceti	Epoch Totals
Recent	0.8	0.0	0 (0)	0 (0)	20 (9)	20 (9)
Pleistocene	1.8	0.8	0 (0)	0 (0)	0 (0)	0 (0)
Pliocene	5.3	1.8	0 (0)	0 (0)	3 (3)	03 (3)
Miocene	24	5.3	0 (0)	2 (1)	18 (9)	20 (10)
Oligocene	34	24	0 (0)	5 (5)	7 (7)	12 (12)
Eocene	56	34	6 (3)	1 (1)	1 (1)	7 (3)
Suborder Totals			6 (3)	8 (5)	44 (20)	

*The Paleocene is not included, since whales did not evolve until the late early Eocene. The boundaries for each epoch are shown in millions of years (Ma), while totals (numbers of species/families) are provided for each epoch. The number of species is listed first, followed by the number of families in parentheses.

the periods in cetacean evolutionary history associated with increases in brain size. Different hypotheses require different patterns of brain evolution at different times, under different conditions, and in different segments of the cetacean phylogenetic tree. Thus, mapping the evolution of brain size on a time-constrained phylogenetic history will lend support to some hypotheses and eliminate others.

The present study is a comprehensive extension of our initial CT-based studies of archaeocete brain size and encephalization. We use CT scanning and postimage processing to calculate endocranial volume and generate three-dimensional reconstructions of endocranial contour for a larger set of fossil cetacean specimens over a wider range of time, including a subset of modern cetaceans. Specifically, the objectives of this study are to (1) measure and document endocranial volume and morphology, along with postcranial indicators of body mass, in individual fossil and modern cetacean specimens; (2) use these data to estimate encephalization level in fossil and modern taxa; and (3) reconstruct the sequence of change in brain size and morphology in cetacean based on our current understanding of the phylogenetic history of this group.

As noted above, some hypotheses about the evolution of cetacean brains make specific testable predictions about when in the evolution of an aquatic lifestyle certain anatomical features of the brain would have developed. The data to be obtained in the present study will form the basis for tests of some of these hypotheses,

particularly when combined with data on other anatomical and environmental factors. Additionally, the present study will yield data on the rate and pattern of cetacean brain evolution that will inform current theories about the uniqueness of the rate and pattern of brain evolution in other phylogenetic groups, including hominids. Finally, as discussed below under our long-term goals, the data from the present study will eventually be considered along with paleoenvironmental data to understand which factors are correlated with increases in encephalization in cetaceans. These

future studies will allow us to address the generality of existing theories about the relationship between various habitat types and encephalization in other mammals.

CETACEAN FOSSIL BRAIN ANALYSIS

Specimen Selection

Most of the samples for this study are part of the fossil vertebrate collections of the United States National Museum (USNM) at The Smithsonian Institution. The collection includes over

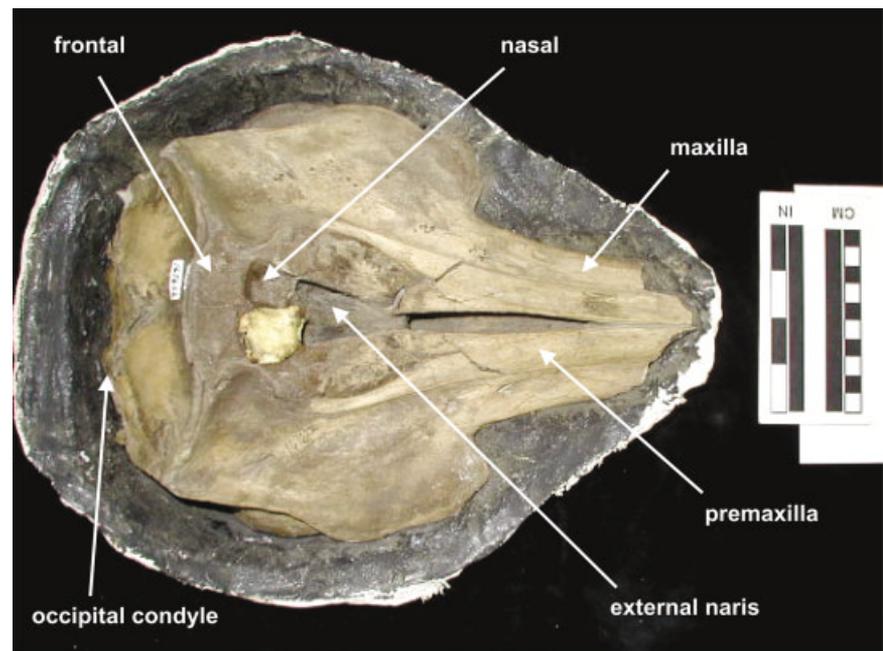


Figure 2. Photograph (dorsal view) of USNM167622, *Eurhinodelphis morrisi*, in plaster of Paris cradle with hardened matrix inside skull visible along the midline openings between the premaxilla. The anterior end of the rostrum is broken and missing. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

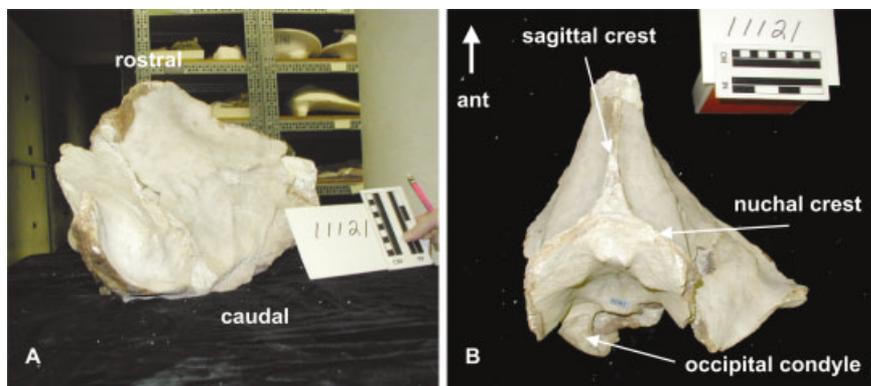


Figure 3. Photographs of USNM 11121 *Basilosaurus cetoides* filled with hardened matrix. **A:** Lateral view. **B:** Dorsal view. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

9,500 fossil cetacean specimens of various sorts ranging from single bones or teeth up to and including virtually complete skeletons. Additional specimens from the Charleston Museum (ChM), the University of Michigan Museum of Paleontology (UMMP), and the Natural History Museum of Los Angeles County (LACM) were studied.

Specimens were selected for this study according to several criteria. First, we chose specimens that spanned from cetacean origins in the Eocene up to and including the recent. Endocranial volume values for recent (modern/extant taxa) specimens included in this study are taken from the literature (Marino, 1998) and also from recent specimens in the vertebrate zoology collection at the USNM.

The second criterion was taxonomic. It would be ideal to include specimens representing all families of fossil and modern cetaceans, but unfortunately some specimens, species, and even entire families could not be included in the study because the specimens were too large to fit into the CT scanner. Most mysticetes were too large to scan, although we have included some small early mysticetes. In addition, larger physeterids (sperm whales) were too large to scan, although some smaller representatives of the Physeteridae were included.

The third criterion for inclusion was quality, which was assessed mainly on completeness of the skull and the lack of any obvious deformation. In addition, because one of our goals is to determine whether changes

in encephalization are related to changes in echolocation and/or hearing ability, specimens with associated periotic bones were favored over those without associated periotics. Another criterion was the nature of the sediment that filled the endocranial cavity. Siliciclastic sediment (sediment composed of silica-rich minerals such as quartz and clay minerals) is much more radiotransparent than carbonate sediment (mainly calcite and other carbonate minerals such as barite and celestite). Thus, specimens preserved in siliciclastic sediment were favored over those preserved in carbonate sediment.

Lastly, specimens were accepted or rejected for inclusion in the study once they were scanned. Any significant deformation that revealed itself

in the scans prompted us to exclude specimens from the study. In addition, if there was poor contrast between the sediment and bone, or if the sediment scattered the x-rays during scanning and created artifacts, specimens were rejected.

The result is a collection of 166 fossil specimens and 50 modern odontocete specimens from which data have been or is being collected. Nine of the fossils are archaeocetes, 15 are mysticetes, 115 are odontocetes, and another 27 have not been identified to suborder as yet, but most are likely to be odontocetes. Due to the difficulty of including the large mysticetes, we decided to focus our study on odontocetes. Table 1 shows the number of species and families represented in each time period and suborder.

Figure 2 depicts a typical odontocete fossil specimen from the Miocene, USNM 167622, *Eurhinodelphis morrisoni*, from Zone 14 of the Calvert Formation, Maryland (approximately 14 Ma). This specimen shows a considerable degree of telescoping, the evolutionary transformation of the skull by which rostral elements elongate, caudal elements move dorsorostrally, and the external nares migrate to the dorsal apex of the skull. Figure 3 depicts photographs (lateral and dorsal views) of a much older archaeocete fossil from the Eocene, USNM 11121, *Basilosaurus cetoides*, from the Ocala Formation, Florida (approximately 37 Ma). The condition of the

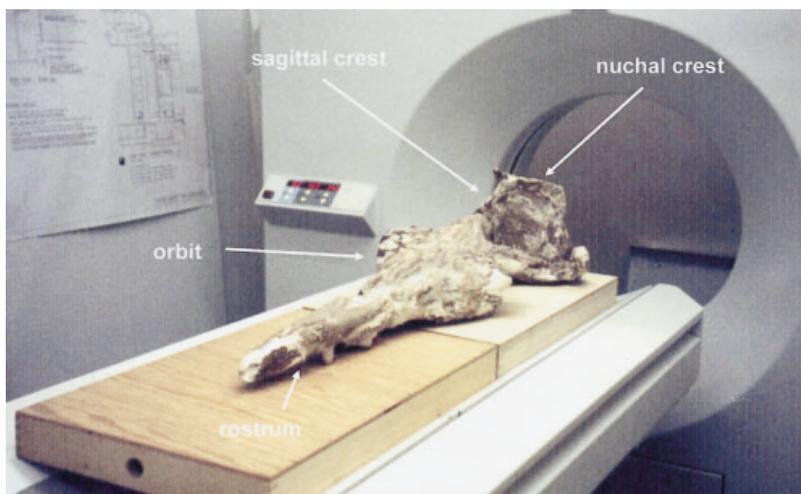


Figure 4. An archaeocete specimen from the Eocene USNM 16638, *Zygorhiza kochii*, in a ventrad position, anterior end pointing away from the scanner, before scanning. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

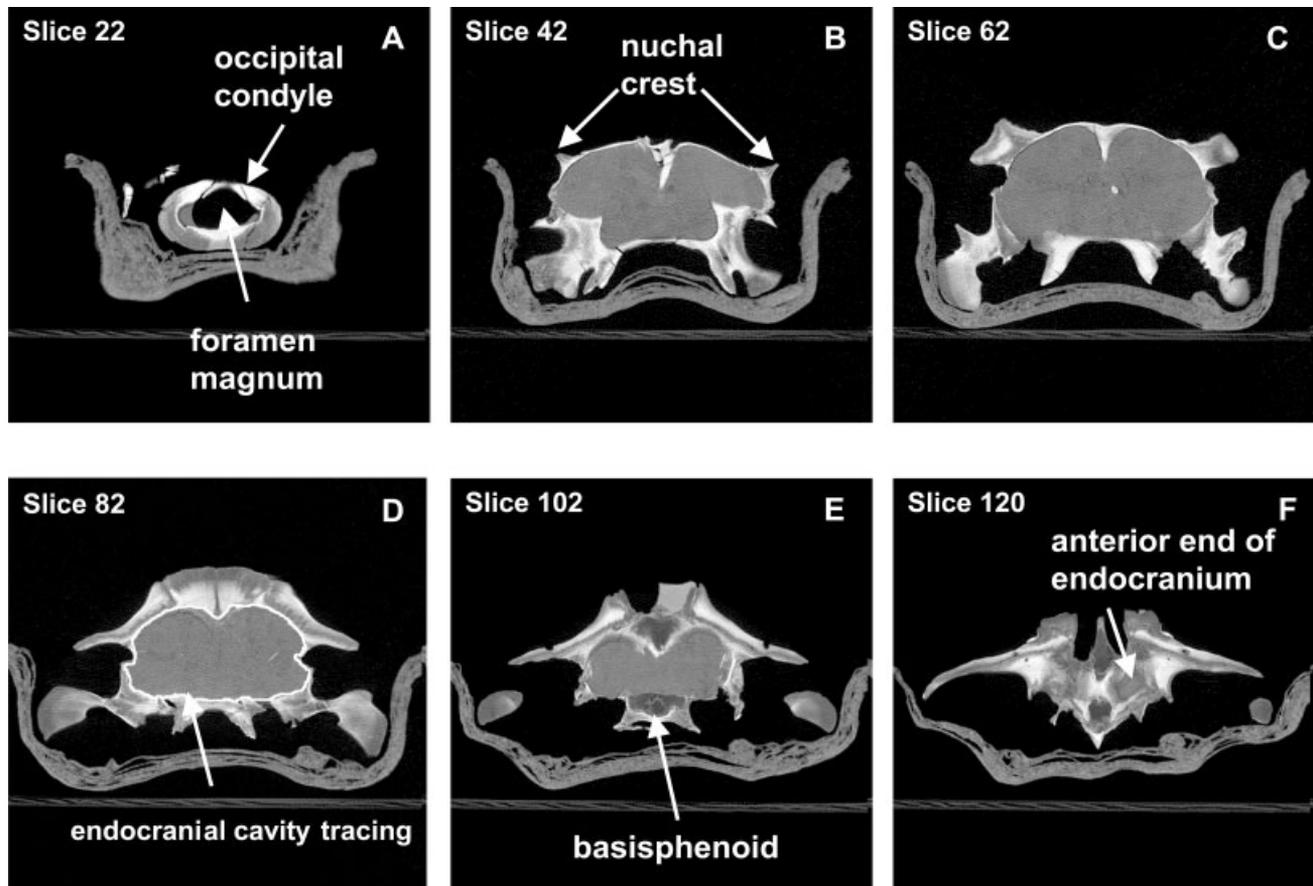


Figure 5. Posterior-to-anterior series of 1.22-mm-thick coronal CT images at 24.4-mm intervals (except for the last, which is 22 mm) through the cranium of USNM 167622, *Eurhinodelphis morrissi*. The endocranial cavity of section 82 is outlined to illustrate how measurements are taken.

specimen in Figure 3 is typical of a specimen dating from the Eocene. Despite being filled with hardened matrix we were able to use CT to measure endocranial volume in this specimen.

CT Scanning Protocol

CT scanning of fossil specimens was conducted using a Siemens Somatom SP scanner located in Bruno Frohlich's laboratory in the Department of Anthropology at the National Museum of Natural History (USNM), Smithsonian Institution. The scanner uses a Sun Sparc microcomputer running Sun OS. Image acquisition, analysis, and file conversions are controlled by Siemens SOMARIS software. OSIRIS software (University Hospital of Geneva) was used to convert Siemens image files into DICOM images. Additional scans were conducted at the Medical University of Charleston in Charleston, South Carolina, on a Marconi MX8000 multiple-slice spiral scan-

ner and at Methodist Hospital in Arcadia, California, on a Picker PQ 5000 single-slice spiral scanner. We obtained contiguous 1- to 2-mm coronal scans of the entire cranium of each specimen 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 surrounding hardened matrix. We scanned the entire specimen past the endocranial cavity as well. Specimens were positioned on the scan table either ventrally or dorsally, depending on which orientation was more stable and so that the posterior end was usually scanned first. Figure 4 shows an archaeocete specimen from the Eocene, USNM 16638, *Zygorhiza kochii*, from the Yazoo Clay Formation (approximately 37 Ma), Choctaw County, Alabama, lying ventrad on the table just before scanning. Figure 5 shows a posterior-to-anterior series of 1.22-mm-thick coronal CT im-

ages at 24.4-mm intervals (except for the last, which is 22 mm) through the cranium of USNM 167622 *Eurhinodelphis morrissi* defining the total endocranial volume. These images show the excellent contrast between fossil skull bone and endocranial matrix.

Measuring Endocranial Volume from CT

We used Scion Image, a PC-based version of NIH Image, and Image J, a Java-based version of NIH Image, to digitally trace around the endocranial cavity on each slice, integrate those areas, and arrive at a volume for the entire endocranial cavity. An outlined coronal section is shown in section 82 of Figure 5. The calculated endocranial volume is an estimate for the size of the brain. For both fossil and modern specimens, the posterior portion of the endocranial region was defined as the most posterior coronal slice

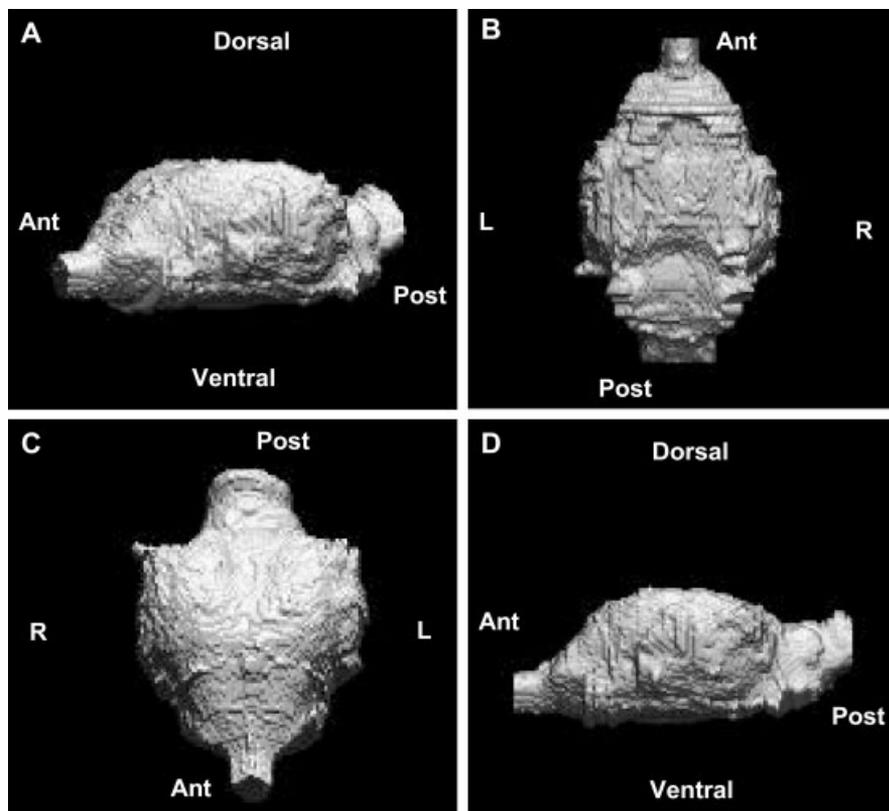


Figure 6. Three-dimensional reconstructions of the endocranial space in specimen ChMPV 4266, *Xenorophus* sp. **A:** Left rostralateral view. **B:** Ventral view. **C:** Dorsal view. **D:** Left lateral view.

containing a completely enclosed foramen. In fossil specimens, the anterior extent was defined as the coronal slice that includes the anterior edge of the basisphenoid or the most anterior coronal slice containing the frontal bone where there is still endocranial space. The use of one or the other of these criteria depended on the cranial morphology (e.g., degree of telescoping) of the fossil specimen. In modern specimens, the anterior extent was defined as the most anterior coronal slice containing the frontal bone where there is still endocranial space.

The total volume of the endocranial space is an overestimate of actual brain size because it includes the volume of the cranial rete mirabile. To estimate brain mass, we are currently estimating the endocranial rete volume from total endocranial volume in each specimen to obtain brain size estimates for use in calculating EQ values. Rete measurements and estimates will be obtained either from the literature, from direct measurement when visible in the CT scans, or by

measuring clay model replicas of endocranial retes on existing natural endocasts.

Estimating Postcranial Parameters

Body mass in fossil mammals has been reconstructed using a variety of methods. These methods rely on a scaling relationship between single or multiple body parts with body mass. Tooth size (particularly molar size) has been used in some mammals that perform a great deal of oral processing of food (Gingerich, 1977). The selected molar is usually one that displays low within-species variability (Gingerich, 1974) in an attempt to maximize its potential correlation with body size. Other methods have used a variety of measurements from long bones to predict body mass (Gingerich, 1990). Because long bones resist the force of gravity on the body mass, their architecture should reflect the ability to resist that force.

Neither of these methods is applica-

ble to fossil cetaceans. Cetacean teeth are not good candidates for a tight correlation with body mass for a variety of reasons. First, most mysticetes lack teeth altogether. Second, most odontocetes do not use their teeth for oral processing, and some, again, lack teeth (Uhen, 2002). Third, even archaeocetes, which retain a more typically mammalian differentiated dentition, have dramatically changed their mode of oral processing from that of their terrestrial ancestors (O'Leary and Uhen, 1999). Besides dentition, long bone dimensions are even less likely to be good predictors of body mass because they no longer resist the force of gravity in fully aquatic cetaceans (Madar, 1998).

Two other methods of estimating body weight have been previously used on fossil cetaceans. First, Jerison (1963) used a method of correlating skeletal length and body mass. In Marino et al. (2000), we adapted this method for use on cetaceans by using modern cetacean skeletal lengths and known body masses to predict fossil cetacean body mass from known skeletal lengths. This method assumes that fossil cetaceans had a body form similar to those of modern cetaceans. This assumption is more likely to be the case for fossil Neoceti and probably even the fully aquatic basilosaurid archaeocetes but less likely to be the case for the earlier semiaquatic archaeocetes. The second method of estimating body weight that has been applied to fossil cetaceans is one developed by Gingerich (1998) that uses a variety of anatomical measurements from the head, vertebral column, and limb elements to estimate body mass. This method uses the relationships of these variables in modern marine mammals to estimate body mass in fossil cetaceans. Although this method shows a great deal of promise, it uses a computer program to perform the calculation, which has not yet been published.

In this study, we use both the body length method and Gingerich's method (at least for those species to which it has been previously applied). We have also added a third method, because very few fossil cetacean specimens (much fewer species) include entire skeletons from which one can obtain a skeletal length or the multi-

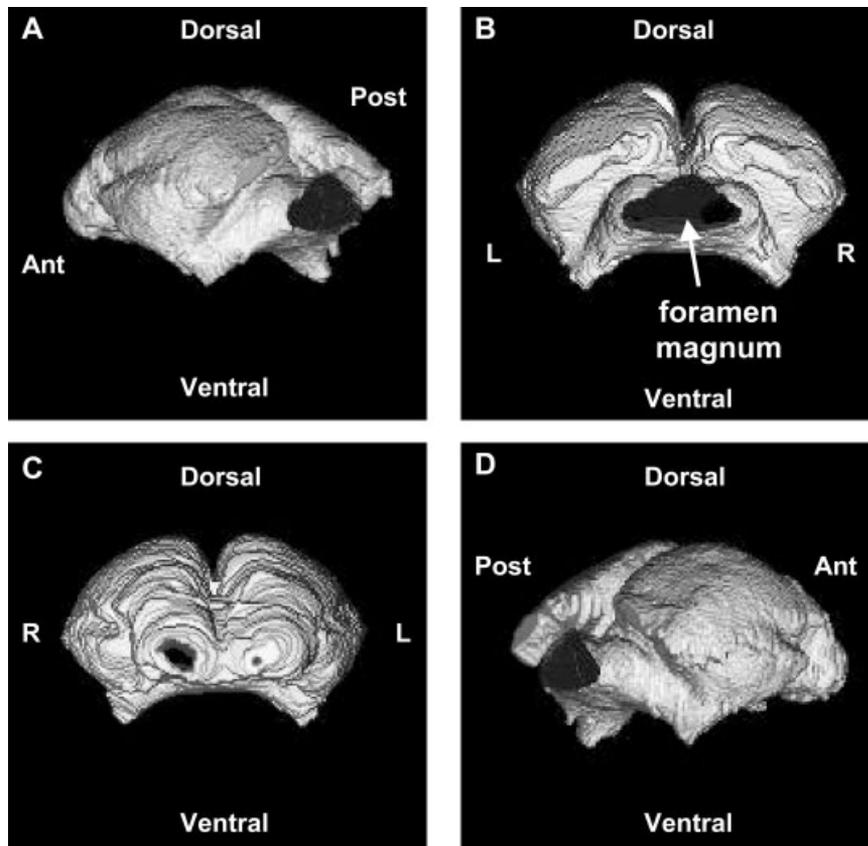


Figure 7. Three-dimensional reconstructions of the endocranial space in specimen USNM 167622, *Eurhinodelphis morrisi*. **A:** Left laterocaudal view. **B:** Caudal view. **C:** Rostral view. **D:** Right laterocaudal view.

ple anatomical measurements needed to apply Gingerich's method. Because specimens were included in our CT study if they had relatively intact crania, we looked for a measurement of the skull that was independent of brain size that might be indicative of body size. We selected the occipital condyle breadth (OCB), because that was the point where the head attached to the body, so we were of the opinion that it had the greatest potential to predict body size of any cranial measurement. We measured the OCB on a wide range of modern cetacean specimens with known body masses and found that it was very strongly correlated with body mass (Pearson $r = 0.89$). This strategy allowed us to use that regression equation to estimate body mass from fossil cetacean specimens where only the cranium is known.

Calculating Encephalization Quotients

As noted previously, encephalization quotient is a measure of observed

brain size relative to expected brain size for a species or genus. EQ values are calculated from a least-squares regression of log mean adult brain weight on log mean adult body weight for a given group. The equation, $EQ = \text{brain weight}/0.12 (\text{body weight})^{0.67}$ from Jerison (1973) was used to derive EQ values for each genus, or when possible, each species, represented in our sample. EQ^{0.67} values for the present sample may be interpreted as loosely expressing how encephalized each genus or species is with reference to a general modern mammalian sample.

Three-Dimensional Reconstruction Through CT

By using Image J software, we assembled our three-dimensional endocranial reconstructions by compiling two-dimensional coronal outlines of the CT-scanned endocrania. These outlines were created by converting the DICOM images to TIFF files using

the OSIRIS program and then tracing the endocranial space on each image with Adobe Photoshop 5.0. The posterior–anterior extent of our outlines were at the opening of the magnum foramen and either the frontal bone (in more recent specimens) or the front region of the endocranium that tapers off rapidly just posterior to olfactory lobe expansion. In some coronal slices where the endocranial area was unbounded or opened by cranial nerves, it was necessary to delimit the endocranial area using consistent endocranial landmarks. The final tracings were then saved in a TIFF format. We loaded the entire set of two-dimensional tracings for each endocranium into Image J, and used Volume Rendering plug-ins to reconstruct the endocranium as a three-dimensional object that could then be viewed at different angles and shading.

Figure 6 displays a three-dimensional reconstruction, in four different views, of the endocranial space in a late Oligocene specimen ChM PV4266, *Xenorophus* sp. from the Chandler Bridge formation, North Carolina (approximately 27 Ma). Figure 7 displays a three-dimensional reconstruction of the endocranial space in specimen USNM 167622, *Eurhinodelphis morrisi* in four different views. Both reconstructions appear to represent the shape of the brain without any obvious distortions. As is the case for most natural and artificial endocasts, it is not possible to detect and reproduce the pattern of convolutions that existed on the surface of the brain. Therefore, interpretations must be based almost entirely on overall shape and morphology of gross structures.

RECONSTRUCTING CETACEAN BRAINS

For the purposes of comparing the reconstructed fossil specimens with a modern cetacean brain, Figure 8, which displays an MRI (Magnetic Resonance Imaging)-based three-dimensional reconstruction of a modern bottlenose dolphin (*Tursiops truncatus*; Field number WAM545) brain from a previously published study (Marino et al., 2001), is reproduced. Because of the recent age of the specimen, some surface convolu-

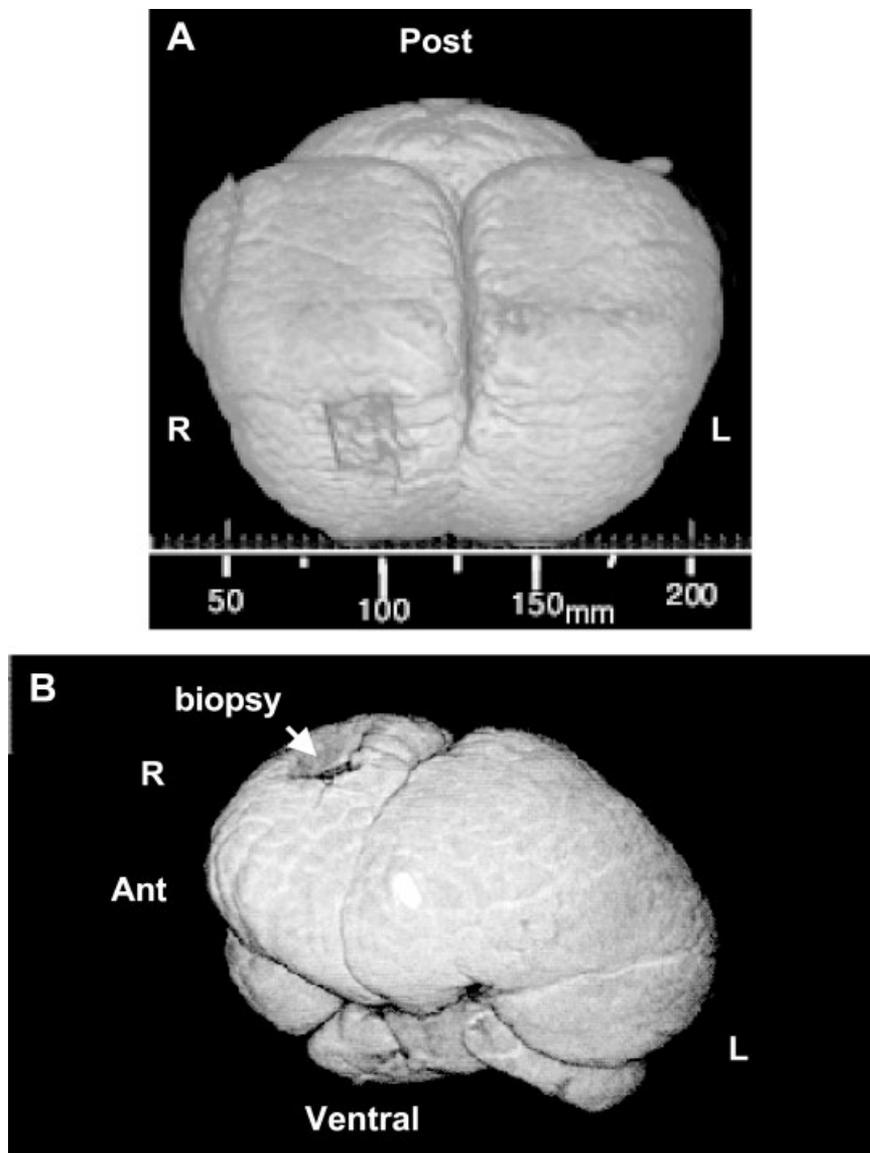


Figure 8. Reproduction of a three-dimensional reconstruction of the endocranial space in a modern bottlenose dolphin specimen (WAM545) from MRI. Dorsal view (A) and rostral left lateral view with ventral side exposed (B), from Marino et al. (2001).

tional patterns are visible on the three-dimensional reconstruction of the bottlenose dolphin but the depth of the gyri and sulci are not well represented.

Although all of the present specimens compared are odontocetes, none of them are related along a single ancestor–descendent lineage. Therefore, the comparisons we make here are for exemplification purposes only and are not meant to suggest direct evolutionary change. Yet, both older fossil specimens (*Xenorophus* sp., ChMPV4266 and *Eurhinodelphis morrissi*, USNM167622) show a lesser degree of cerebral elaboration than

the modern specimen (*Tursiops truncatus*, WAM545). There is a gradation of cerebral development ascertainable across all three, with the oldest specimen ChMPV 4266, showing the least amount of bulbousness characteristic of modern odontocete brains. ChMPV 4266 displays the more elongated appearance of archaeocete and earlier cetacean specimens. Notably, the reconstructions show that the olfactory bulbs of the 27 million-year-old ChMPV 4266 are still intact but that they are considerably regressed and essentially vestigial in the more recent 14 million-year-old USNM 167622 and completely gone in the modern

specimen. Generally, the overall morphology of the cerebral hemispheres of the more recent *Eurhinodelphis* specimen more closely resembles the modern odontocete brain than the older *Xenorophus* specimen.

The EQ values associated with ChMPV 4266, USNM 167622, and the modern bottlenose dolphin, are approximately 3.28, 2.67, and 4.14, respectively. All of these values indicate that the three specimens had brains larger than expected for their body size. However, these EQ values do not show a pattern of increasing encephalization similar to the pattern of increased morphologic development observed. This is likely because there was a wide range of encephalization levels throughout most of cetacean evolution (with values ranging from less than 1 to more than 4.5) and these specimens do not reflect an ancestor–descendent lineage. The point here is

Apart from modern humans, cetaceans are the most highly encephalized mammals that have likely ever existed.

that these kinds of reconstructions, considered with encephalization estimates, can serve as the basis for much more highly detailed and quantitative morphologic comparisons of the proportions and organization of whole brains and brain structures across specimens that, when registered to our best estimate of phylogenetic relations, can inform us directly about the pattern of change that occurred in various cetacean lineages.

BRAIN ELABORATION, BEHAVIOR, AND FUNCTION

Cetacean brain evolution is an intriguing example of how large complex brains can emerge from ordinary beginnings. As noted above, apart from modern humans, cetaceans are the most highly encephalized mammals that have likely ever existed. The encephalization level of many modern

odontocete species, particularly in the Delphinid and Phocoenid families, approach modern human levels. This level of brain elaboration exceeds that achieved by even our closest phylogenetic relatives, the great apes (Marino, 1998). At the same time, we know from modern comparative studies and also from emerging fossil-based data that the large brains of cetaceans evolved along a strikingly different trajectory from other mammalian brains and, notably, from primate brains (Glezer et al., 1988). The differences between cetacean and primate brains exist at the level of gross morphology, lobular arrangement, proportions of subcortical structures, and neocortical cytoarchitecture (Glezer et al., 1988, for a review). There is also a prodigious body of literature demonstrating the complex nature of cetacean intelligence (Herman, 1986; Reiss et al., 1997; Marino, 2002) that rivals and converges with the abilities of the great apes. For instance, bottlenose dolphins share the same extremely rare capacity for mirror self-recognition with great apes and humans (Reiss and Marino, 2001). Therefore, by exploring the divergent evolutionary natures of cetacean and primate brains, we have an exciting opportunity to probe questions about alternative neuroanatomical avenues to complex cognitive abilities.

The application of new noninvasive imaging technologies, such as computed tomography, have already brought the study of primate and hominid brain evolution to a new level (Zollikofer et al., 1998). Here, we have demonstrated how the same methods can elucidate cetacean brain evolution and, thereby, make possible the kinds of interesting comparative questions mentioned above. For the first time, we can address specific hypotheses about selective forces and temporal patterns in cetacean brain evolution through CT-based analyses of brain morphology. This approach will bring new rigor to the study of brain size and morphologic evolution in cetaceans and, thereby, new insights into the neuroanatomical basis of cetacean behavior and intelligence.

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