Endocranial Volume of Mid-Late Eocene Archaeocetes (Order: Cetacea) Revealed by Computed Tomography: Implications for Cetacean Brain Evolution

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The large brain of modern cetaceans has engendered much hypothesizing about both the intelligence of cetaceans (dolphins, whales, and porpoises) and the factors related to the evolution of such large brains. Despite much interest in cetacean brain evolution, until recently there have been few estimates of brain mass and/or brain–body weight ratios in fossil cetaceans. In the present study, computed tomography (CT) was used to visualize and estimate endocranial volume, as well as to calculate level of encephalization, for two fully aquatic mid-late Eocene archaeocete species, *Dorudon atrox* and *Zygorhiza kochii*. The specific objective was to address more accurately and more conclusively the question of whether relative brain size in fully aquatic archaeocetes was greater than that of their hypothesized sister taxon Mesonychia. The findings suggest that there was no increase in encephalization between Mesonychia and these archaeocete species.

KEY WORDS: archaeocete; endocranial volume; encephalization; computed tomography; Cetacea.

INTRODUCTION

Cetaceans (dolphins, whales, and porpoises) are large brained, fully aquatic mammals second only to modern humans in relative brain size when brain–body allometry is taken into account (Marino, 1998; Ridgway and Tarpley, 1996; Worthy and Hickie, 1986). One measure of relative brain size is the encephalization quotient (EQ), a measure of relative brain size, which takes into account the allometric relationship between brain and body size. The EQ values for at least five species (*Grampus griseus*, *Delphinus delphis*, *Lagenorhynchus obliquidens*, *Tursiops truncatus*, and *Sotalia fluviatilis*) within the fam-

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ily Delphinidae of the suborder Odontoceti range between 4.0 and 4.6 (Marino, 1998). These delphinids possess a brain more than four times the expected mass compared with other mammals, second only to modern humans with an EQ of 7.0.

The large brain of modern cetaceans has engendered much hypothesizing about both the intelligence of cetaceans and the factors related to the evolution of such large brains (Connor *et al.*, 1998; Eisenberg, 1986; Glezer *et al.*, 1988; Herman, 1986; Jerison, 1978, 1986; Marino, 1996; Ridgway *et al.*, 1966; Ridgway and Wood, 1988; Worthy and Hickie, 1986). Cetacean evolution was accompanied by major transformations in cranial and postcranial morphology (Barnes, 1985; Buchholtz, 1998; Gaskin, 1982; Luo, 1998; Luo and Gingerich, 1999; Oelschlager, 1990). It is tempting to consider the transition from a terrestrial to a fully aquatic existence as the impetus for all of these changes, particularly the substantial increase in relative brain size which characterizes cetacean evolution. Until recently there have been few estimates of brain mass and/or brain-body weight ratios in fossil cetaceans because of difficulty accessing the hardened matrix, which fills many endocranial cavities of fossil whales. However, Dart (1923) estimated brain mass from endocranial casts in *Dorudon atrox* (= *Zeuglodon intermedius*) as 785 cc and in another specimen of the same species (= *Prozeuglodon atrox*) as greater than 800 cc because the anterior end was missing. Dart (1923) also reported endocranial volumes for three specimens of *Saghacetus osiris* (= *Zeuglodon osiris*, = *Zeuglodon elliotsmithii*, = *Zeuglodon sensitivus*) specimens as 470, 310, and 490 cc, respectively. Jerison (1973, 1978) used Dart's endocranial volume values along with estimates of body size to obtain EQ values (with respect to terrestrial mammals) of 0.61 for *S. osiris*, 0.73 for one specimen of *D. atrox*, and 0.05 for another *D. atrox* specimen. The discrepant EQ value of 0.05 was due to the fact that Jerison used a body size estimate for *D. atrox* that was actually that of the much larger *Basilosaurus isis*. In addition, these earlier studies involved overestimates of brain mass from endocranial volume because they did not take into account that total endocranial volume is comprised of nonneural tissue as well as brain mass. Marples (1949) and Breathnach (1955) showed that much of what Dart (1923) interpreted as brain mass was actually a large intracranial vascular rete mirabile. This vascular complex can sometimes comprise nearly 20% of total endocranial volume (see below).

More recently, Gingerich (1998) used natural endocasts to reinterpret brain and body mass for *S. osiris*, *D. atrox*, and *B. isis*, from endocranial volumes of 485, 1200, and 2800 cc, respectively, taking into account estimates of endocranial rete volume. Gingerich used these brain mass estimates to calculate an EQ value for each species, which was based on a modern mammalian regression curve very similar to that used by Jerison (1973). The respective resulting brain mass estimates of 388, 960, and 2520 cc for *S. osiris*, *D. atrox*, and *B. isis*, combined with body mass estimates, yielded EQ values of 0.49, 0.51, and 0.37, respectively. In addition, Gingerich (1998) calculated EQs of 0.25 and 0.29 for the middle Eocene archaeocetes *Rodhocetus kasrani* and *Dalanistes ahmedi*, respectively. Recently, Bajpai *et al.* (1996) reported an estimated brain volume of less than 290 cc for the mid-Eocene archaeocete *Indocetus ramani* and remarked on the small size of the cerebrum from the endocast dimensions. These earlier studies by Dart (1923) and Jerison (1973, 1978), along with Bajpai et al. (1996) and the more recent EQ estimates employing a correction factor for endocranial rete volume by Gingerich (1998), suggest that at least some archaeocete species were less encephalized than the average modern terrestrial mammal.

The best candidates for archaeocete terrestrial ancestry are the Paleocene and early Eocene Mesonychia, which possess morphological, temporal, and geographical similarities to archaeocetes (Gingerich, 1998). Gingerich (1998) calculated EQ from brain and body mass estimates for two mesonychid species, middle Eocene *Mesonyx obtusidens* (Radinsky, 1976) and early Eocene *Pachyaena ossifraga.* He obtained EQ values of 0.40 to 0.51 for *M. obtusidens* and 0.18 for *P. ossifraga* using an empirically based equation, which yielded a regression slope of 0.74 and a *y* intercept of 0.062. When the brain and body weight values for these two specimens are used to calculate EQ based upon the equation by Jerison (1973), which yields a slope of 0.67 and intercept of 0.12, the EQ values obtained are 0.2 for *P. ossifraga* and 0.44–0.55 for *M. obtusidens.* Comparison of the archaoecete EQ values with those for these two mesonychids suggests that archaeocetes did not enjoy a substantial increase in relative brain size over their terrestrial ancestors. However, the current archaeocete EQ values must be tentatively considered because they are based on nonuniform measures of endocranial volume and a small sample size.

In recent years, computed tomography (CT) has proved to be an important tool in the study of fossil endocranial features because it is nondestructive and enables more accurate, precise, and reliable measurement of endocranial features than traditional methods (Conroy and Vannier, 1984, 1985, 1986; Conroy *et al.*, 1990). Gingerich *et al.* (1994) were the first to utilize CT to study endocranial features in a fossil marine mammal, the middle Eocene sirenian *Protosiren fraasi.* In the present study, CT-based endocranial volume is used to calculate an estimated EQ for two contemporary fully aquatic mid-late Eocene archaeocete species, *Dorudon atrox* and *Zygorhiza kochii.* The specific objective is to more accurately and more conclusively address the question of whether relative brain size in fully aquatic archaeocetes was greater than than of ancestral Mesonychia. The more general theoretical question addressed is that of whether a land-to-water transition per se was associated with increased encephalization in the cetaceans or whether other potentially more direct and important factors are associated with increased encephalization in cetaceans.

MATERIALS AND METHODS

The *Dorudon atrox* sample, recently described by Uhen (1996), in the present study consists of three specimens for which endocranial data were obtained from CT scanning. In addition, six specimens for which endocranial volume was obtained directly from the natural endocasts (Uhen, 1996) were included to provide additional data on *D. atrox.* The *Zygorhiza kochii* sample in the present study, originally described by Kellogg (1936), consists of two specimens for which endocranial data were obtained from CT scanning. Figure 1 is an illustration of three views of the skull of *D. atrox* (a composite based upon UM101222, UM93220, and UM100139)[8]; Fig. 2 displays a photograph of the skull of *Z. kochii* (USNM16639). Figure 3 displays a composite illustration of the *D. atrox* brain from endocasts, which includes a depiction of the rete mirabile.

A General Electric HiLight Advantage System was used to create 5-mm contiguous

[8] Museum abbreviations used in this study are: NHML, Natural History Museum, London; UM, University of Michigan Museum of Paleontology; USNM, United States National Museum of Natural History, The Smithsonian Institution.
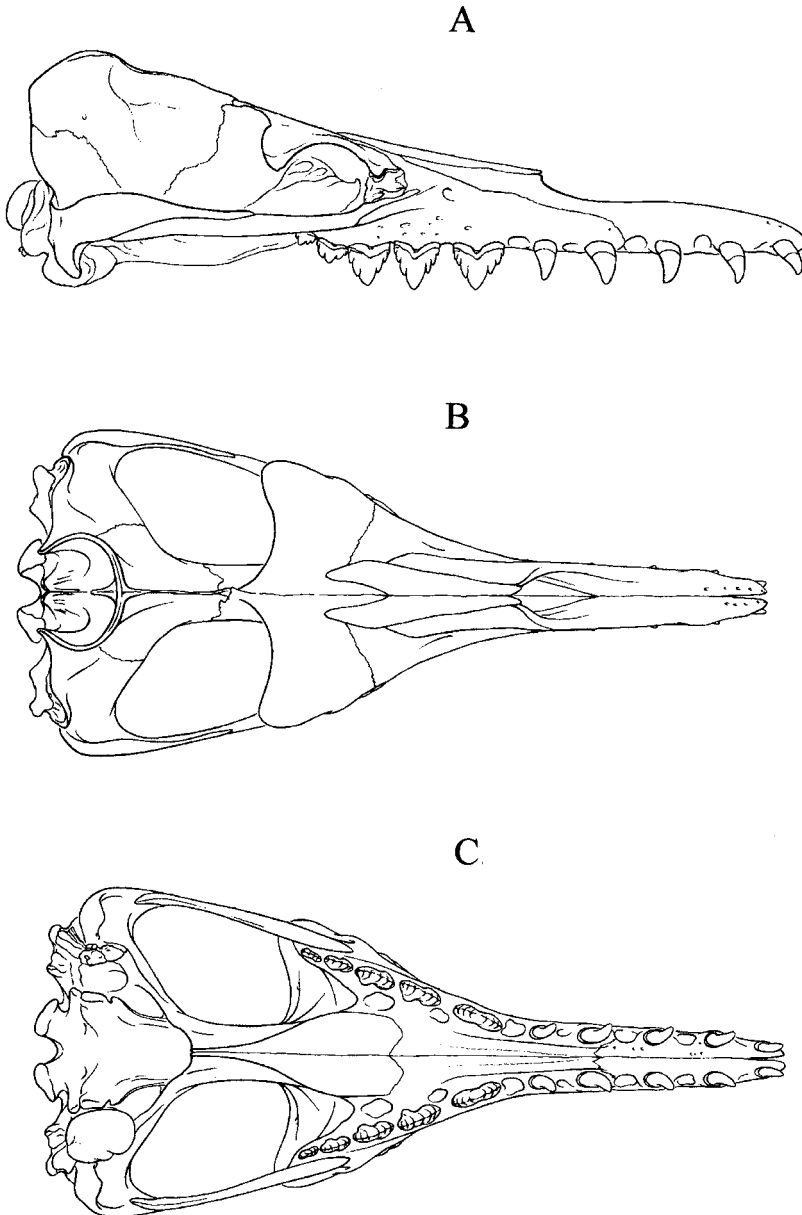
A

B

C

Fig. 1. Illustration of (A) lateral, (B) dorsal, and (C) ventral views of the skull of *Dorudon atrox* (a composite based upon UM101222, UM93220, and UM100139).

coronal CT images at 120–140 kV at 140–280 mA through the entire cranium of the three scanned *D. atrox* specimens. Volumetric measurements were made using the GE HiLight software. For the *Z. kochii* specimens, a Siemens Somatom AR.T scanner was used to create 2-mm contiguous coronal images at 110 kV at 210 mA through the entire cranium of both
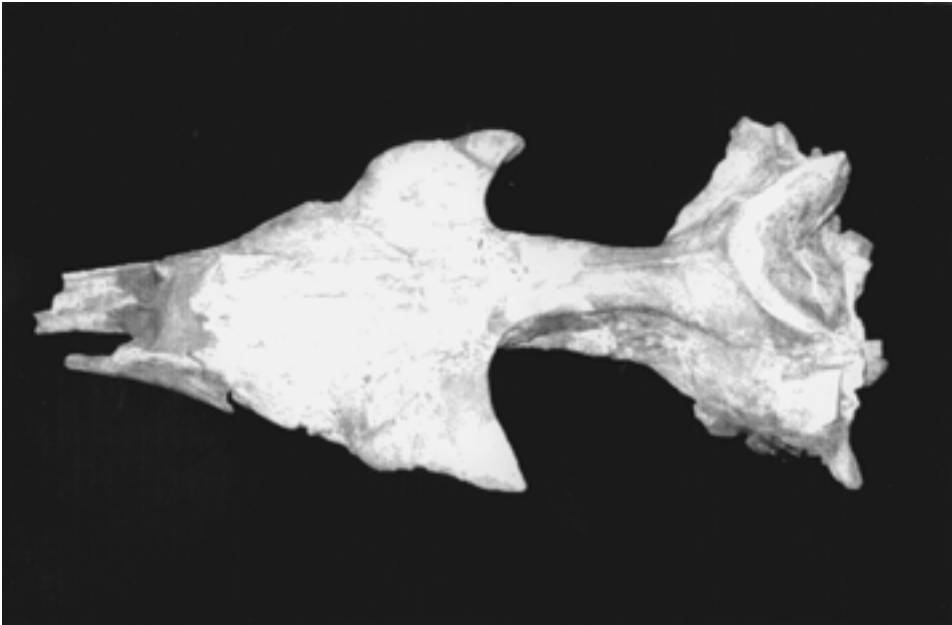
Fig. 2. Photograph of dorsal view of the skull of *Zygorhiza kochii* (USNM16639).

specimens. Scion Image, a PC-based version of NIH Image, was used to conduct volumetric measurements from the images. For both *D. atrox* and *Z. kochii* the posterior portion of the endocranial region was defined as the most posterior slice containing a completely enclosed foramen magnum and the anterior extent was defined as the slice that includes the anterior edge of the basisphenoid. Endocranial volume was calculated for each specimen by tracing the inner edge of the braincase in all digitized CT sections within the defined endocranial region. The area of each closed trace was computed and multiplied by the slice spacing (5 mm for *D. atrox* and 2 mm for *Z. kochii*) to represent the volume associated with each trace. A total volume was obtained by adding volumes associated with the individual slices within the defined endocranial region. For *D. atrox* three sets of measurements were made by Mark Uhen (MU) and the average values used to calculate total endocranial volume. An intraclass correlation coefficient, which measures the homogeneity of scores across ratings, was calculated as a measure of intrarater reliability for the *D. atrox* measurements. For one of the *Z. kochii* specimens, three sets of measurements were made by MU and one set jointly by Lori Marino (LM) and John Matthew Aldag (JMA), whose measurements were combined into one set, LM/JMA. An intraclass correlation coefficient was calculated as a measure of intrarater reliability for MU's *Z. kochii* measurements. Interrater reliability between MU's mean measurements of *Z. kochii* and that of LM/JMA was assessed by intraclass correlation as well. The average of the four sets of measurements was used to calculate total endocranial volume for *Z. kochii.*

Each specimen of *D. atrox* was assigned to an age class based on dental eruption sequence and tooth wear (Uhen, 1996). The *Z. kochii* specimens were assigned to an age class based on the dental eruption sequence described by Uhen (2000). Body mass for
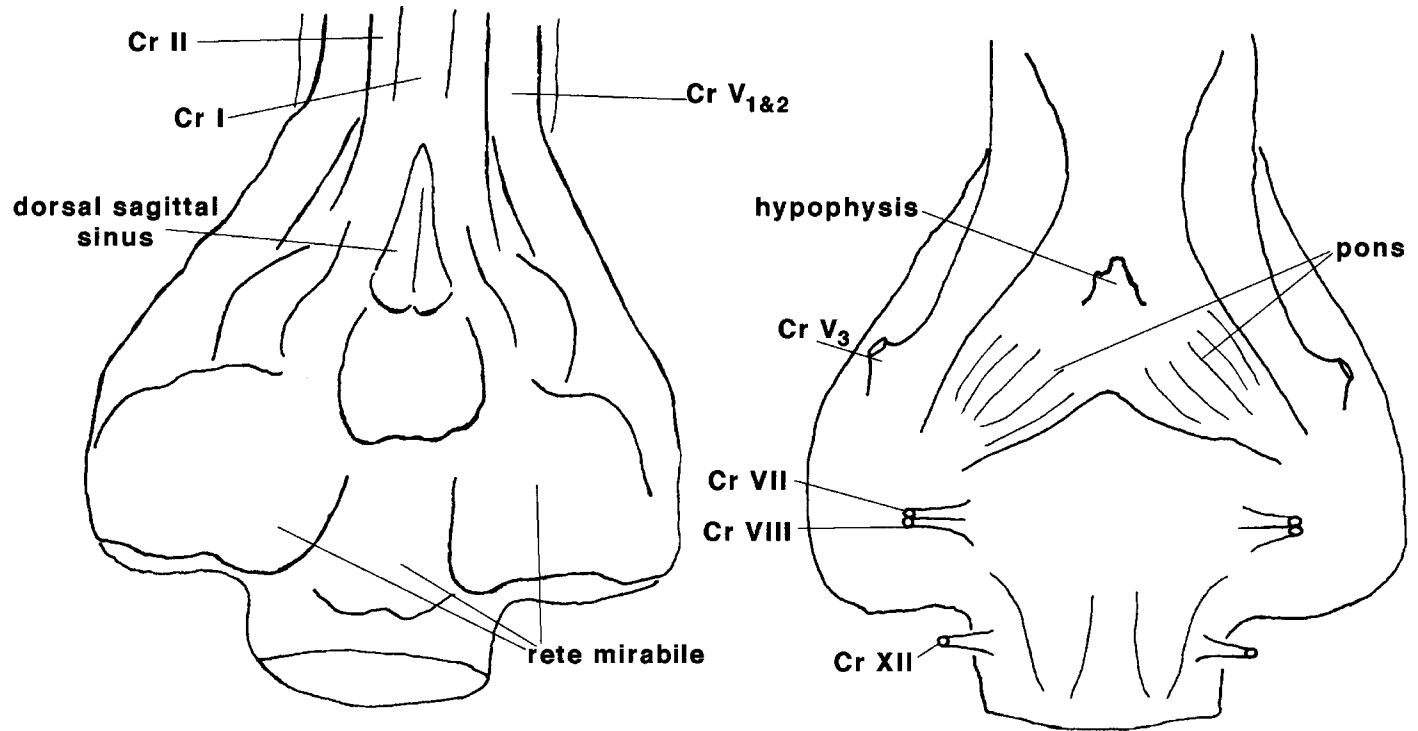
Fig. 3. Illustration of dorsal and ventral views of the brain endocast of *Dorudon atrox* displaying the dorsal sagittal sinus, hypophysis, pons, rete mirabile, and cranial nerves I, II, $V_{1,2,3}$, VII, VIII, XII.

D. atrox was estimated from two relatively complete adult *D. atrox* specimens (UM101215 and UM101222) by constructing a regression equation, based on a method developed by Jerison (1963), to predict body mass from skeletal length. Skeletal lengths of modern cetaceans were collected from several sources (Nishiwaki and Kamiya, 1958; Omura, 1958, 1975; Omura *et al.*, 1981) and personal observations of author MU. The skeletal lengths were correlated with body masses from Silva and Downing (1995) to construct a regression equation predicting log body mass from log skeletal length. The resulting regression equation was: logBM = 3.08(logSL) − 4.84, where BM is body mass in kilograms and SL is skeletal length in centimeters. Based on an estimated adult skeletal length from UM101215 and UM101222 of 485 cm, this equation was used to estimate adult body mass of *D. atrox* as 2700 kg. Based on an estimated skeletal length of 520 cm from an adult *Z. kochii* specimen [USNM11962 (Kellogg, 1936)], adult body mass for *Z. kochii* was estimated as 3351 kg.

The total volume of the endocranial space is an overestimate of actual brain size because it includes the volume of the cranial rete mirabile. In order to obtain an accurate estimate of endocranial rete volume, molds were made of the rete of five of the six *D. atrox* specimens (NHML M9265, UM 93235, UM 93234, UM 94795, and UM 94796). While the anterior, posterior, and dorsal surfaces of the casts made from these molds reflect the actual extent of retial tissue, there is no bony structure showing the division between the dorsal surface of the cerebrum and the ventral surface of the rete mirabile. To estimate the position of this surface, the ventral surface of each rete mirabile cast was sculpted to match the contour of the dorsal surface of the cerebrum visible anterior and posterior to the rete mirabile on the cranial endocasts. The volume of the rete mirabile casts was then measured using water displacement. The average retial volume of the five specimens was 19.5% of the total endocranial volume. This percentage was used to estimate brain weight for those specimens (NHML M10173, UM 97506, UM 100139, UM 101222, USNM 16638, and USNM 16639) for which endocranial volume was based upon CT scans.

In order to converge upon the best estimate of EQ in *D. atrox* and *Z. kochii* and to facilitate comparisons with other species, EQ was calculated for the present fossil sample in two ways. First, a least-squares regression of brain weight on body weight for members of the modern cetacean suborder Odontoceti was used as a reference for calculating EQ from estimated brain and body weight for the fossil sample. In this analysis, *D. atrox* and *Z. kochii* EQs will reflect their level of encephalization relative to modern cetaceans. Second, a least-squares regression of brain weight on body weight for a large sample of mammals from Jerison (1973) was used as a reference for calculating EQ from estimated brain and body weight for the fossil sample. In this second analysis, *D. atrox* and *Z. kochii* EQs will reflect their level of encephalization relative to a more general modern mammalian group. Only data from adult *D. atrox* and *Z. kochii* specimens were used in calculating EQ estimates. Endocranial volume estimates from juvenile specimens were examined, however.

RESULTS

Figure 4 shows 5-mm thick coronal CT images through the cranium of one *Dorudon atrox* specimen (UM100139) at 15-mm intervals from the most posterior slice to the most anterior slice defining the total endocranial volume. Figure 5 shows 2-mm thick coronal CT images of one *Zygorhiza kochii* specimen (USNM16638) at 20-mm intervals from
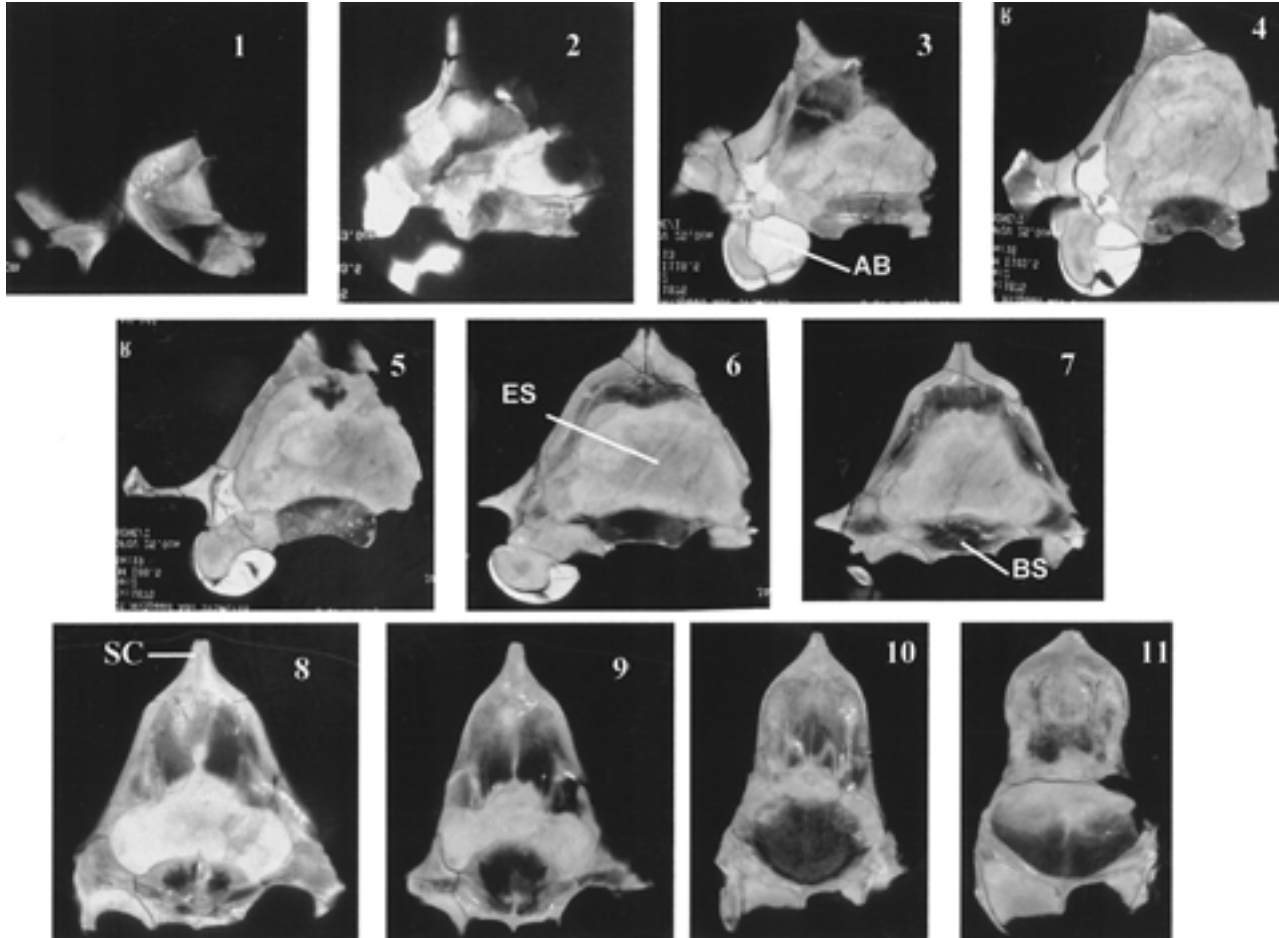
Fig. 4. Coronal CT images through *Dorudon atrox* (UM100139), specimen at 15-mm intervals from the most posterior slice to the most anterior slice defining the total endocranial volume. ES = endocranial space, BS = basisphenoid, AB = auditory bulla, SC = sagittal crest.
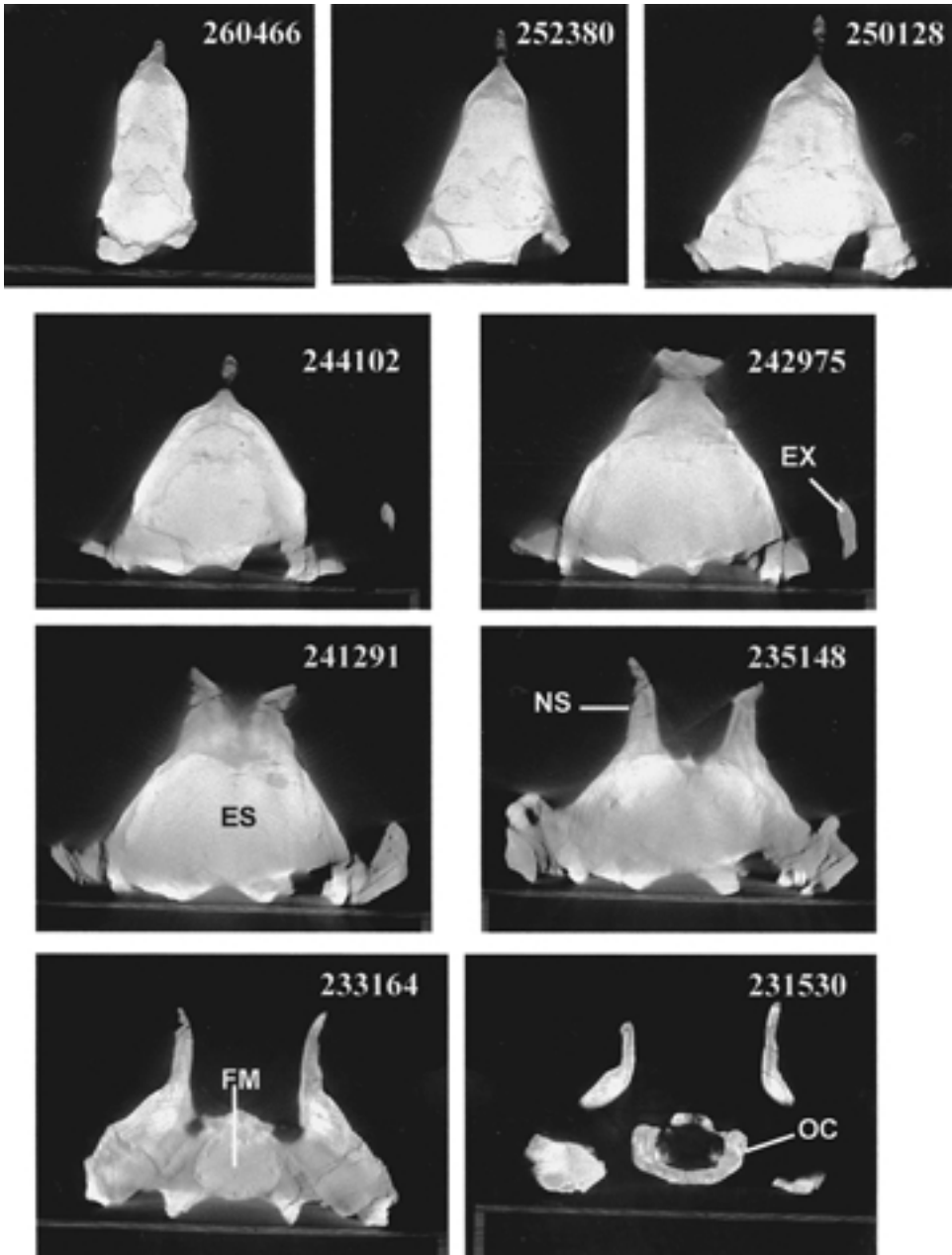
Fig. 5. Coronal CT images of *Zygorhiza kochii* cranium (USNM16638) at 20 mm intervals from the most posterior slice to the most anterior slice defining the total endocranial volume. The last two images are 16 mm apart. ES = endocranial space, OC = occipital condyle, FM = foramen magnum, EX = exoccipital, NS = nuchal crest.

Table I. Age Class, Calculated Endocranial Volume, Estimated Rete Mirabile Volume, and Estimated Brain Weight for Each Specimen

Specimen	Age class[a]	Endocranial volume (cm^3)	Rete mirabile volume (cm^3)	CT scan (cm^3)	Estimated brain weight	Retial % of total
Dorodun atrox						
NHML M9265	4	800.0	135.8		664.2	17.0
NHML M10173	4	785.0	153.1		631.9	
UM 93235	3	1046.0	245.2		800.8	23.4
UM 93234	1	780.0	126.3		653.7	16.2
UM 94795	5	1170.0	245.1		924.9	20.9
UM 94796	4	1225.0	246.7		978.3	20.1
UM 97506	4		189.2	970.0	780.8	
UM 100139	1		97.5	500.0	402.5	
UM 101222	10		228.7	1173.0	944.3	
Zygorhiza kochii						
USNM 16638	10		178.8	917.0	738.2	
USNM 16639	7		146.4	751.0	604.6	

[a]Age classes: 1–9, juvenile to subadult; 10, adult.

the most posterior slice to the most anterior slice defining the total endocranial volume. The last two images are 16 mm apart.

The intraclass correlation coefficient for MU's three endocranial volume measures for the *D. atrox* specimens is 0.91. The intraclass correlation coefficient for MU's three measures of the *Z. kochii* specimen is 0.98. These results show that the intrarater reliability for *D. atrox* and *Z. kochii* was extremely high. The intraclass correlation coefficient for the *Z. kochii* measurements made by LM/JMA and MU's averaged measurements is 0.92. This value indicates that there was very high agreement between raters on the *Z. kochii* measurements.

Table I lists each specimen in the present study along with its age class, calculated endocranial volume, estimated rete mirabile volume, and estimated brain weight (i.e., estimated rete mirabile volume subtracted from calculated endocranial volume). Because the specific gravity of brain tissue is nearly one, volumetric units are replaced by weight units.

Figure 6 graphically displays the range of estimated brain sizes as a function of age class for *D. atrox* and *Z. kochii. Dorudon atrox* brain size estimates range from 402.5 g for UM100139 in the first age class to 978.3 g for UM94796 in age class four. The general pattern reveals increasing brain size estimates with age in *D. atrox* and, despite the small sample size, in *Z. kochii.*

EQ for *D. atrox* was calculated using the estimated brain weight of 944.3 g for UM101022 and a body weight of 2700 kg. Only UM10122 was chosen because EQ changes with maturation and this was the only adult specimen that could contribute to an estimate of adult EQ for this species. EQ for *Z. kochii* was calculated using the estimated brain weight of 738.2 g for USNM16638 and a body weight of 3351 kg. A least-squares regression of brain weight on body weight for a sample of 21 modern odontocetes was used as a reference for calculating EQ from estimated brain and body weight for the fossil sample (Marino, 1995). The resulting regression equation was used to calculate an
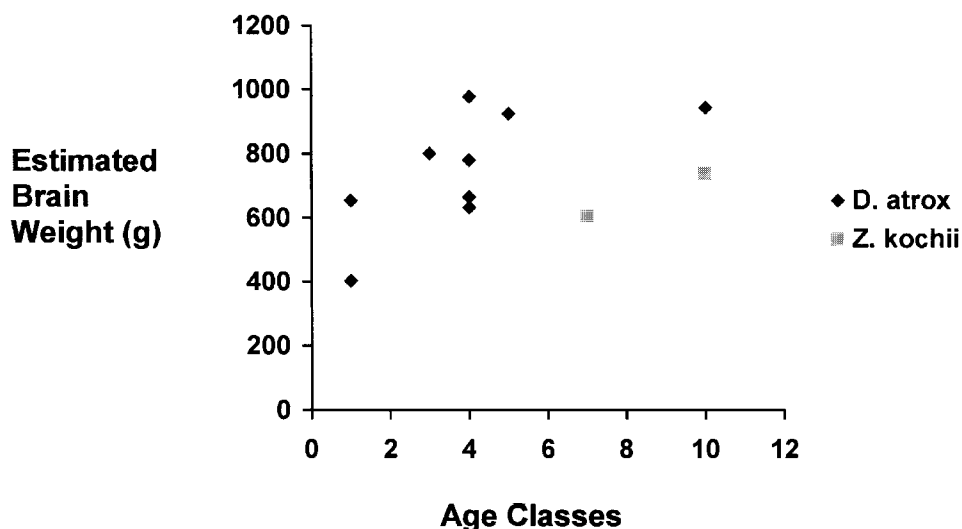
Fig. 6. Graph of the range of estimated brain weights as a function of age class for *Dorudon atrox* and *Zygorhiza kochii*.

EQ for *D. atrox* and *Z. kochii*, whereby EQ = brain weight/1.6 (body weight)$^{.53}$. These analyses indicate that the EQ of *D. atrox* was about 0.23 and that the EQ of *Z. kochii* was about 0.16, compared with modern odontocetes.

A least-squares regression of brain weight on body weight for a large sample of modern mammals from Jerison (1973) was used as a reference for calculating a second EQ from estimated brain and body weight for the fossil sample. Jerison's regression equation, EQ = brain weight/.12 (body weight)$^{.67}$, was used to calculate an EQ for *D. atrox* based on UM10122 and *Z. kochii* based on USNM16638. The resulting EQ values represent the EQ of *D. atrox* and *Z. kochii* compared with modern mammals. Based on these analyses, the EQ of *D. atrox* and *Z. kochii* was about 0.39 and 0.26, respectively.

DISCUSSION

The present analysis confirms that reliable measures of endocranial volume can be obtained for fossil archaeocetes using CT methodology. The present study is also the first to include an estimate of EQ in *Zygorhiza kochii*. The EQ estimates of 0.16 compared with modern odontocetes and 0.26 compared with a large set of modern mammals show that *Z. kochii* was below average in encephalization. In the present study, EQ for *Dorudon atrox* was calculated as 0.23 compared with modern odontocetes and 0.39 compared with modern mammals. The EQ value for *D. atrox* using Jerison's (1973) regression equation is somewhat lower than that obtained by Gingerich (1998) using a similar equation, but it still reveals that *D. atrox* was not highly encephalized. One caveat to the comparison between *D. atrox* and *Z. kochii* and most modern odontocetes is that the two archaeocete species possess larger bodies than most species of the modern six-family odontocete comparison group. Therefore, the EQ values of the archaeocetes in this

study may be somewhat suppressed when compared with modern odontocetes. Indeed, the very large modern sperm whale (*Physeter macrocephalus*), with an EQ of 0.58, also possesses a lower EQ than other modern odontocetes ostensibly because of its disproportionately large body size (Marino, 1998). Larger body sizes without a proportionate increase in brain size may occur in fully aquatic animals because they lack the gravitational constraints placed upon the bodies of terrestrial mammals. In the present study, *P. macrocephalus* was not included in the regression analysis on which the *D. atrox* and *Z. kochii* EQ values were based for this reason. Nevertheless, when the brain weight to body weight ratio of *D. atrox* and *Z. kochii* is compared with a modern odontocete within the same body size range as these archaeocetes, i.e., *Ziphius cavirostris*, it is clear that *D. atrox* and *Z. kochii* are not as highly encephalized as this modern species. *Ziphius cavirostris* possesses an EQ of 0.54 (Marino, 1998) compared with other modern odontocetes (compared with 0.24 and 0.16 for *D. atrox* and *Z. kochii*, respectively) and 0.92 using Jerison's (1973) equation (compared with 0.40 and 0.26 for *D. atrox* and *Z. kochii*, respectively).

In relation to their putative terrestrial ancestors, the present results suggest that *D. atrox* and *Z. kochii* were no more encephalized than Mesonychia. EQ values of 0.44 to 0.55 and 0.2 for the mesonychians *Mesonyx obtusidens* and *Pachyaena ossifraga*, respectively, are not significantly different than the EQ values of 0.39 for *D. atrox* and 0.26 for *Z. kochii.* A comparison of the archaeocete EQ values with those for these two mesonychids suggests that archaeocetes did not enjoy a substantial increase in encephalization over their terrestrial ancestors. It is important to note that these conclusions are not dependent upon the estimates of endocranial rete volume. When no endocranial rete volume is subtracted and total endocranial volume is used in calculating EQ, the results lead to the same conclusion. In this case, the EQ, based on Jerison's equation, for *D. atrox* is 0.48 and for *Z. kochii* 0.32. Therefore, even when the largest estimates of brain size are used, these archaeocetes are still well within the range of encephalization of their purported ancestors.

Despite the small sample size upon which EQ estimates are based, the present study adds considerably to our limited knowledge of brain size in two archaeocete species, *Dorudon atrox* and *Zygorhiza kochii*, using highly reliable and precise CT imaging methods. We anticipate that this methodology will facilitate future studies of endocranial morphology and volume in fossil cetaceans and other mammals.

The present findings have important implications for our understanding of how and why major evolutionary transitions occur and suggest that we must look elsewhere than towards the transition to a fully aquatic existence as the basis for increased encephalization in cetaceans. It appears 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. For example, modern cetacean brain size is correlated with social group size (Marino, 1996). Perhaps, socially based pressures served as the impetus for increased brain size in cetaceans. On a related note, some authors have suggested that increased encephalization is related to the evolution of echolocation and a complex communication system (Bateson, 1966; Jerison, 1986; Worthy and Hickie, 1986). In the future, data from the fossil record bearing on the evolution of brain size and morphology, sound production and reception, and other characteristics, should be integrated so that a more complete picture of cetacean evolution can emerge.

ACKNOWLEDGMENTS

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