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Africanacetus from the sub-Antarctic region: The southernmost record of fossil beaked whales

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We report two partial skulls of fossil beaked whales (Odontoceti, Ziphiidae) of uncertain age trawled from the sea floor of the sub-Antarctic Indian Ocean (58 to 60°S), representing the southernmost record of the family. The skulls possess diagnostic features of the genus *Africanacetus*, several specimens of which have been recovered from the sea floor off South Africa, but differ from the type and only known species *Africanacetus ceratopsis* in their larger size. This difference may either reflect intraspecific variation or indicate the existence of a hitherto unrecognised species. The two specimens are characterised by unusually developed mesorostral ossifications, combined with maxillary crests occurring in the facial region. Both of the latter are found in a range of extant and extinct ziphiids, and known to be sexually dimorphic in extant beaked whales. These structures may be the result of hypermorphosis driven by sexual selection, and could be involved in male-specific behaviour.

Key words: Mammalia, Cetacea, Ziphiidae, hypermorphosis, sexual selection, Antarctic.

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Introduction

Beaked whales (Odontoceti, Ziphiidae) are a diverse family of cetaceans generally occupying open-water and deep-water habitats, and their fossil remains are frequently dredged from the sea floor (e.g., Whitmore et al. 1986; Bianucci et al. 2007). The Southern Hemisphere record of extinct ziphiids was recently greatly expanded by the description of an exceptionally diverse, possibly Miocene assemblage recovered from the sea bed off the coast of South Africa (Bianucci et al. 2007, 2008). Among the species identified in the South African assemblage, the most abundantly represented was *Africanacetus ceratopsis* Bianucci, Lambert, and Post, 2007, which recent phylogenetic analyses suggest to be closely related to the extant genera *Hyperoodon* and *Mesoplodon* (subfamily Hyperoodontinae sensu Muizon, 1991 or subtribe Hyperoodontina sensu Moore, 1968). Here, we describe two new specimens of fossil ziphiids trawled from the bottom of the sub-Antarctic Indian Ocean, and refer them to the genus *Africanacetus.* In addition, we provide a discussion of their morphology, and their implications for the geographical distribution of the genus.

Material and methods

In 1976, fragments of two fossil cetacean skulls were trawled from the sea floor by the vessel *Karadag* in the southern part of Banzare Bank in the sub-Antarctic Indian Ocean (approximately 58 to 60°S, 74 to 81°E; exact coordinates unknown). The specimens are housed in the museum of the South Scientific Research Institute of Marine Fisheries and Oceanography, Kerch, Ukraine and consist of proximal portions of rostra with associated fragments of the facial region up to the external nares (maxilla, premaxilla, and vomer) (Figs. 1–4). Measurements are listed in Table 1. Our anatomical terminology follows Mead and Fordyce (2009).

Institutional abbreviations.—YugNIRO, South Scientific Research Institute of Marine Fisheries and Oceanography, Kerch, Ukraine; SAM, Iziko South African Museum, Cape Town, South Africa.

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Table 1. Cranial measurements (in mm) of *Africanacetus* sp. from Banzare Bank. Asterisks indicate estimated values.

Measurement	YugNIRO 408	YugNIRO 409
Length of rostral portion of maxilla	390+	300+
Maximum width of mesorostral groove	54	47
Width of rostrum at prominential notch	195	189
Width of rostrum at antorbital notch	290*	314*
Width of premaxillae at prominential notch	108	87
Preorbital width of skull	390+	350+
Width between apices of dome-shaped maxillary crests	165	194
Maximum width of vomer	54*	47
Maximum height of rostrum	140	116+
Distance between large maxillary (dorsal infraorbital) foramina	131	136
Distance between maxillary tubercles	251	287
Distance from apex of left dome-shaped maxillary crest to sagittal midline	–	104
Distance from apex of right dome-shaped maxillary crest to sagittal midline	–	118
Distance from apex of left dome-shaped maxillary crest to midline of rostrum at the level of the maxillary tubercles	–	108
Distance from apex of right dome-shaped maxillary crest to midline of rostrum at the level of the maxillary tubercles	–	138

Systematic palaeontology

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Family Ziphiidae Gray, 1850

Subfamily Hyperoodontinae Gray, 1866

Genus *Africanacetus* Bianucci, Lambert, and Post, 2007

Type species: *Africanacetus ceratopsis* Bianucci, Lambert, and Post, 2007; trawled from the Atlantic sea floor off the coast of South Africa; Neogene.

Africanacetus sp.

Material.—YugNIRO 408–409, partial skulls including portions of the rostrum.

Age and horizon.—Unknown. Previous studies derived tentative Neogene age estimates for trawled specimens of fossil ziphiids from associated phosphorites (Bianucci et al. 2007). However, no phosphate concretions are present on the surface of the specimens described here, and no Neogene events of phosphorite formation have been described for Banzare Bank (Burnett and Riggs 1990; Baturin 2004).

Description.—The two skulls are larger than *Africanacetus ceratopsis* (Bianucci et al. 2007, 2008) and comparable in size to the extant *Indopacetus pacificus* (Dalebout et al. 2003), suggesting a total body length of about 6 m (Table 1). All of the sutures are well fused, indicating that the specimens represent adult individuals.

The rostrum is high and robust, and only slightly narrows anteriorly in dorsal view (Fig. 1). In lateral profile (Fig. 3), it is similar to that of the extant *Mesoplodon densirostris* and *M. europaeus*, but much wider transversely and more robust. While damage to the ventral surface prevents any precise estimate of the height of the rostrum for either specimen, its proximal portion seems to have been at least as high as wide. The vomer is pachyosteosclerotic (i.e., both dense and swollen) within the rostrum, as well as in the ventral narial region (Fig. 5), and completely fills the mesorostral groove. As in *A. ceratopsis*, the vomer bears a median suture and is strongly elevated above the dorsal margin of the premaxilla, overhanging the latter along its entire preserved length. In lateral view, the part of vomer elevated above the premaxilla and maxilla accounts for about one half of the total height of the rostrum.

The rostral part of the premaxilla is transversely narrow and fused to the vomer along a barely visible suture. As in *A. ceratopsis*, the premaxillary sac fossa is shallow and slopes laterally. In anterior view, the premaxillary foramina are located slightly dorsal to the maxillary (dorsal infraorbital) foramina. The suture between the maxilla and premaxilla is visible, but mostly obliterated owing to fusion of these two bones. Posterolaterally, the rostrum terminates in a shallow prominential notch bordered laterally by a small maxillary tubercle. The lateral margin of the maxilla is distinctly keeled along the rostrum and ascends towards the prominential notch.

As in *A. ceratopsis*, a low crest runs posteriorly from the maxillary tubercle, joining a more posteromedially situated, dome-shaped maxillary crest at its posterior end. The dome-shaped crest has a steep medial and a gradually sloping lateral margin, giving the maxilla a “bird-wing” profile in anterior or posterior view. This profile is distinct from the symmetrical, semi-rounded maxillary crests in the extant *Hyperoodon planifrons*. The anteromedial portion of the facial region of the skull is slightly asymmetrical, with the facial portion of the right maxilla being larger than its counterpart on the left. This results in the right maxillary crest being located more posterolaterally than the left one, as can be seen when comparing measurements 12/13 and 14/15 (Table 1).

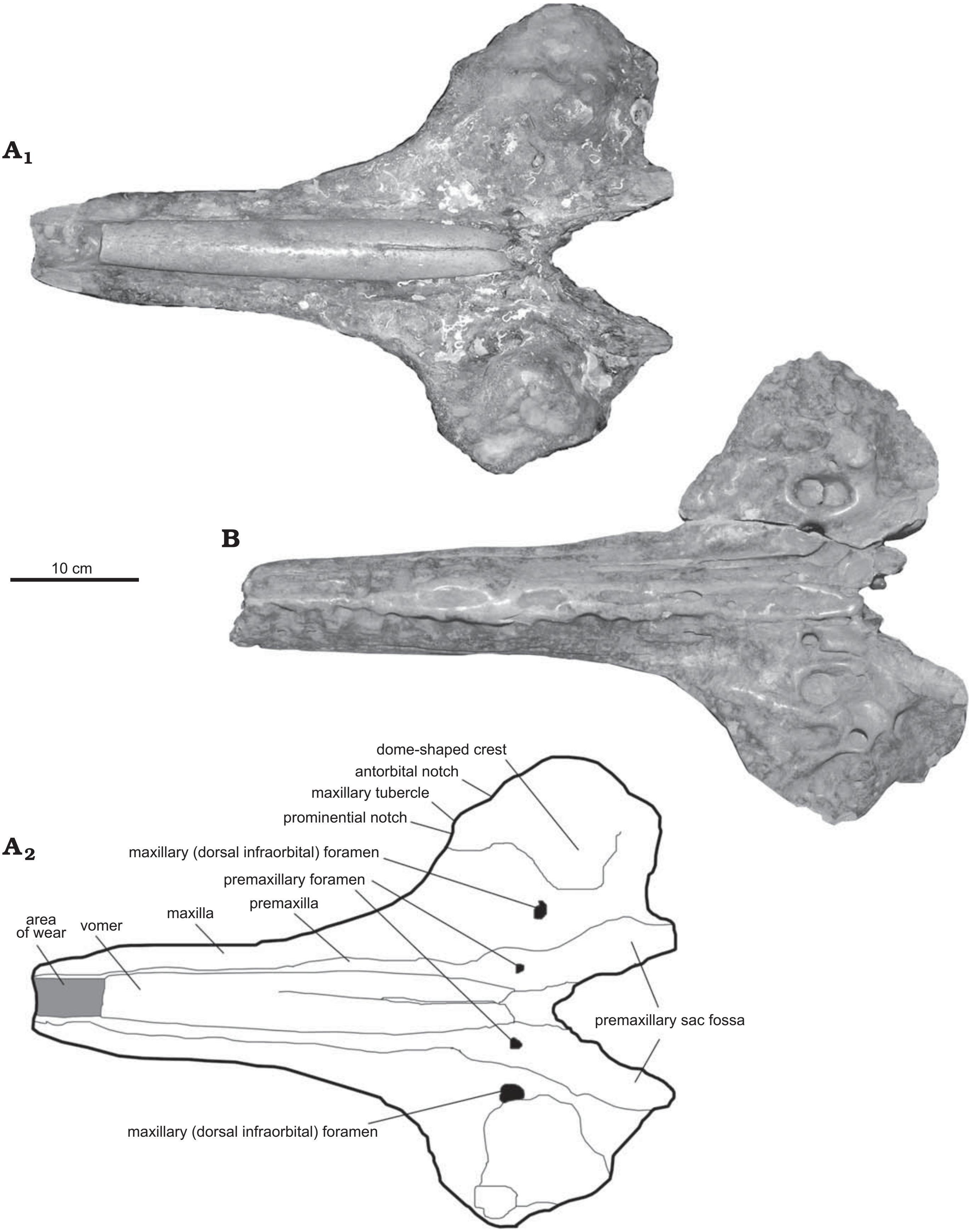

Fig. 1. The beaked whale *Africanacetus* sp., skull in dorsal view. **A**. YugNIRO 409, photograph (A_1) and explanatory drawing (A_2). **B**. YugNIRO 408.

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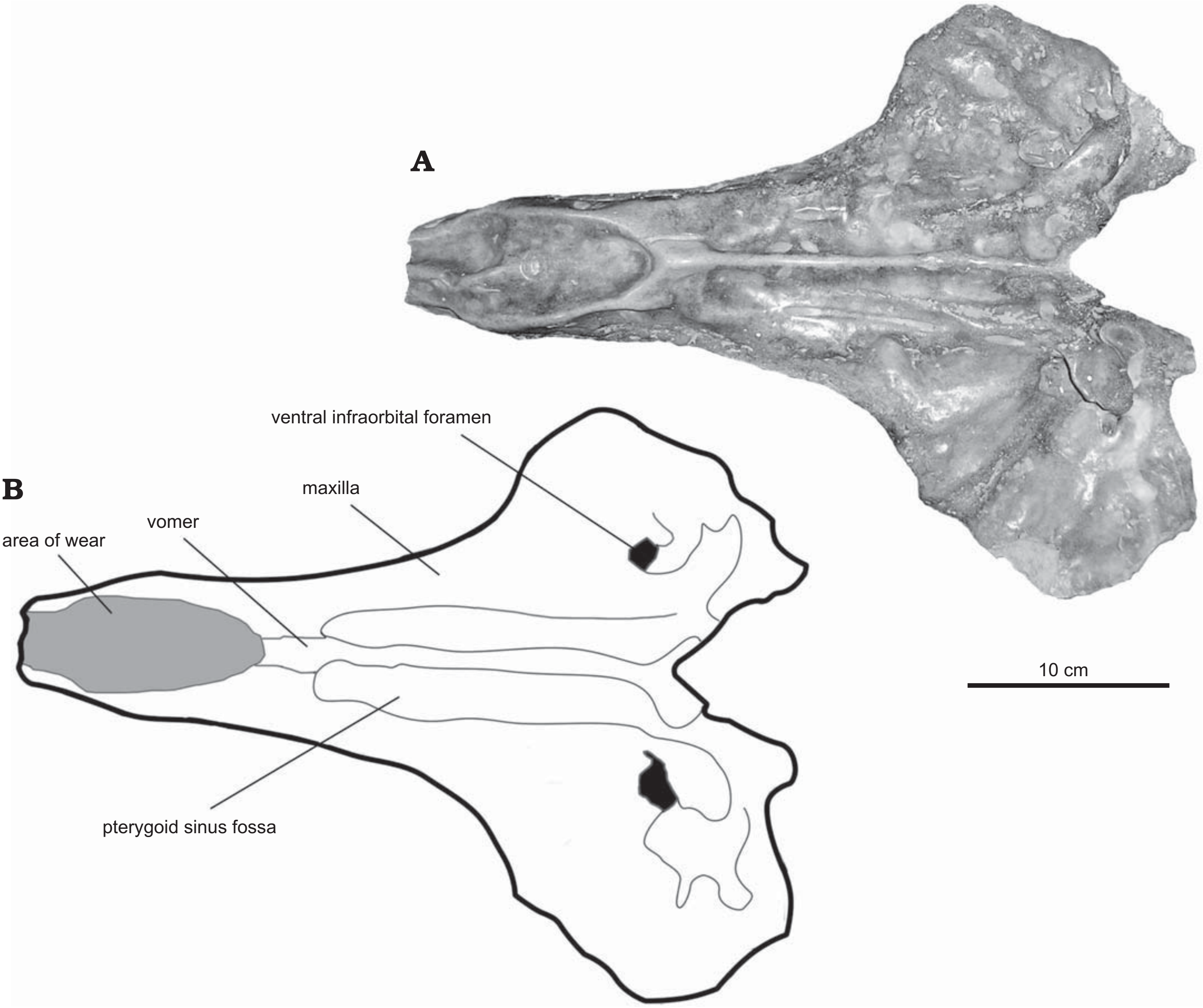

Fig. 2. The beaked whale *Africanacetus* sp., skull (YugNIRO 409) in ventral view. **A**. Photograph. **B**. Explanatory drawing.

On the ventral surface of the rostrum, the pterygoid sinus fossa extends to a point approximately 90–100 mm anterior to the prominential notch. Extensive wear and damage has obliterated most of the other morphological details. The maxilla-palatine suture is not visible, likely owing to the poor state of preservation of the bone surface.

Discussion

Comparison with the type series and variation.—While the two skulls described here share with *Africanacetus ceratopsis* the presence of a dome-like maxillary crest and a laterally sloping premaxillary sac fossa to the exclusion of all other described ziphiid taxa, they are larger than other specimens assigned to this species. This difference is particularly evident in the antorbital region, where the width of the rostrum at the level of antorbital notch is about 1.5 times greater than in the three specimens of *A. ceratopsis* for which measurements have been reported (Bianucci et al. 2007). The Banzare Bank skulls further differ from the holotype of *A. ceratopsis* in their more developed mesorostral ossification of the vomer, although, as pointed out by Bianucci et al. (2007), this trait is highly variable among the specimens reported from South Africa.

These differences are either the result of intraspecific variation, arising from differences in age, ecology, geographical distribution and/or sexual dimorphism, or may indicate the existence of a separate species. The range and limits of within-species variation of cranial measurements are insufficiently studied for cetaceans in general. Although large amounts of data were obtained for many species, published summaries are

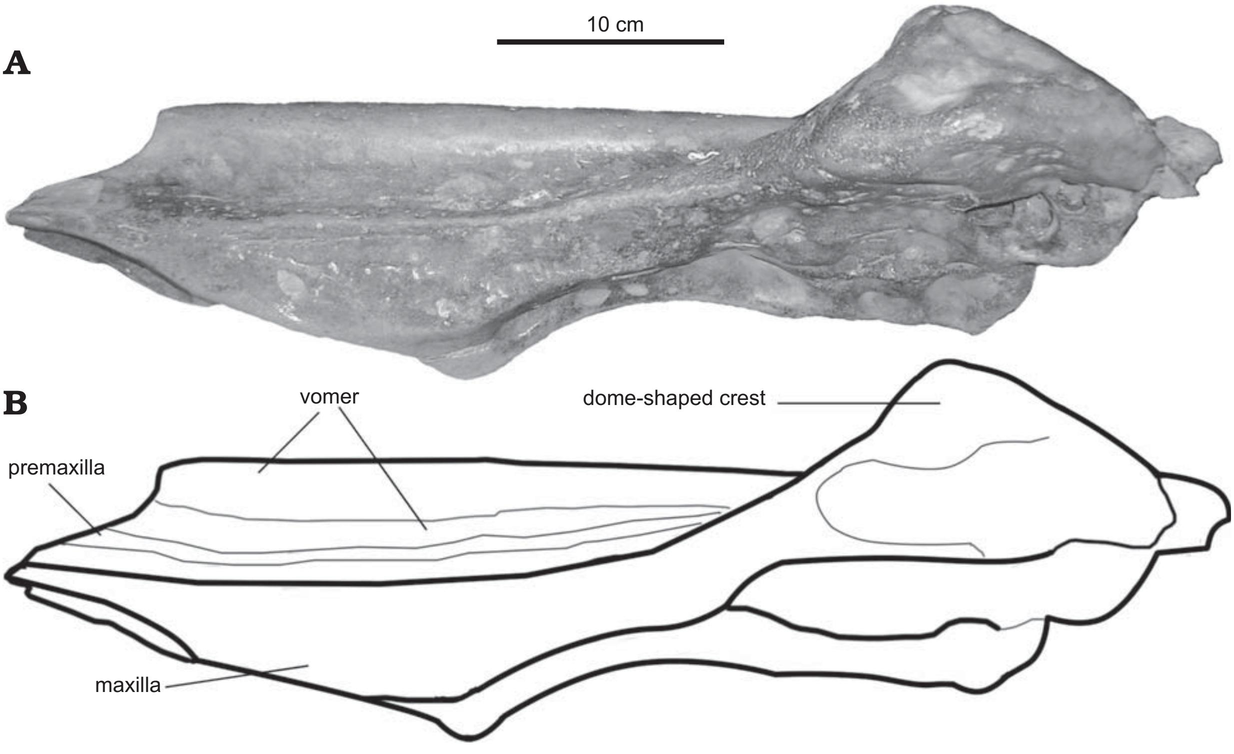

Fig. 3. The beaked whale *Africanacetus* sp., skull (YugNIRO 409) in lateral view. **A**. Photograph. **B**. Explanatory drawing.

scarce. One of the most comprehensive works is the monograph by Perrin (1975) describing variation in spotted dolphins (*Stenella attenuata*) and spinner dolphins (*S. longirostris*). While the latter analysis found age to be the most important factor in determining intraspecific variation, it also identified some considerable individual differences among adults in terms of, for example, the preorbital width of the skull, or the width of the nares and rostrum (see Perrin 1975: table 13a). Variation on a similar scale is observed in the harbour porpoise *Phocoena phocoena* across geographical regions (PG, personal observation). While both sexual dimorphism and geographical or ecological (ecotype or subspecies) differences contribute to this variation, the latter seem to be the more important determinants of size in small delphinoids (Perrin 1975). By contrast, strong sexual dimorphism is characteristic of some extant ziphiids. In particular, the observed size variation in *Africanacetus* is comparable to that seen among adults of the northern bottlenose whale *Hyperoodon ampullatus* (Hardy 2005), with large old males having skulls about 1.5 larger than females. Sex and probably age as causes for variation are further corroborated by a link between the latter and the development of the mesorostral ossification in extant and fossil beaked whales (see below).

Based on the high degree of bone fusion and the occurrence of bony structures, we identify the present specimens as adult males, and it is therefore possible that they may represent new occurrences of *Africanacetus ceratopsis*. Nevertheless, the size difference between the new material and the previously described specimens of *A. ceratopsis* remains remarkably great. Taken together with the fact that at least one specimen of *A. ceratopsis* (SAM PQ 3002; Bianucci et al. 2007) shows a level of mesorostral ossification comparable to the Banzare Bank skulls despite being smaller than the latter, and given the additional uncertainty regarding the age of both the new specimens and the type series of *A. ceratopsis*, the possibility of a new species can therefore not be excluded. Indeed, pairs or complexes of closely related species differing in body and skull size are widespread across mammalian taxa, including cetaceans (e.g., *Kogia breviceps* and *K. simus*, *Phocoena spinipinnis* and *P. sinus*), and closely related species of extant beaked whales usually display similar body sizes (see, for example, the molecular phylogeny of *Mesoplodon* of Dalebout et al. 2008). Based on these considerations, any more definite referral of the fossils from Banzare Bank must await the discovery of more complete material.

Unusual mesorostral ossification combined with facial skull crests.—The presence of a mesorostral ossification formed by the vomer is well documented for the extant genera *Mesoplodon* and *Ziphius*, as well as several extinct ziphiids (Lambert 2005; Bianucci et al. 2007, 2008; Lambert et al. 2011). In those extant taxa in which it occurs, the mesorostral ossification is strongly sexually dimorphic and considerably more developed in adult males (e.g., True 1910; McCann 1965; Moore 1968; Besharse 1971; Heyning 1984; MacLeod and Herman 2004). Proposed explanations for the function of the mesorostral ossification (MacLeod 2002; Lambert et al. 2011) range from diving ballast (Buffrénil and Casinos 1995; Buffrénil et al. 2000) to sound transmission (Zioupos et al. 1997; Cranford et al. 2008; Buffrénil and Lambert 2011) and

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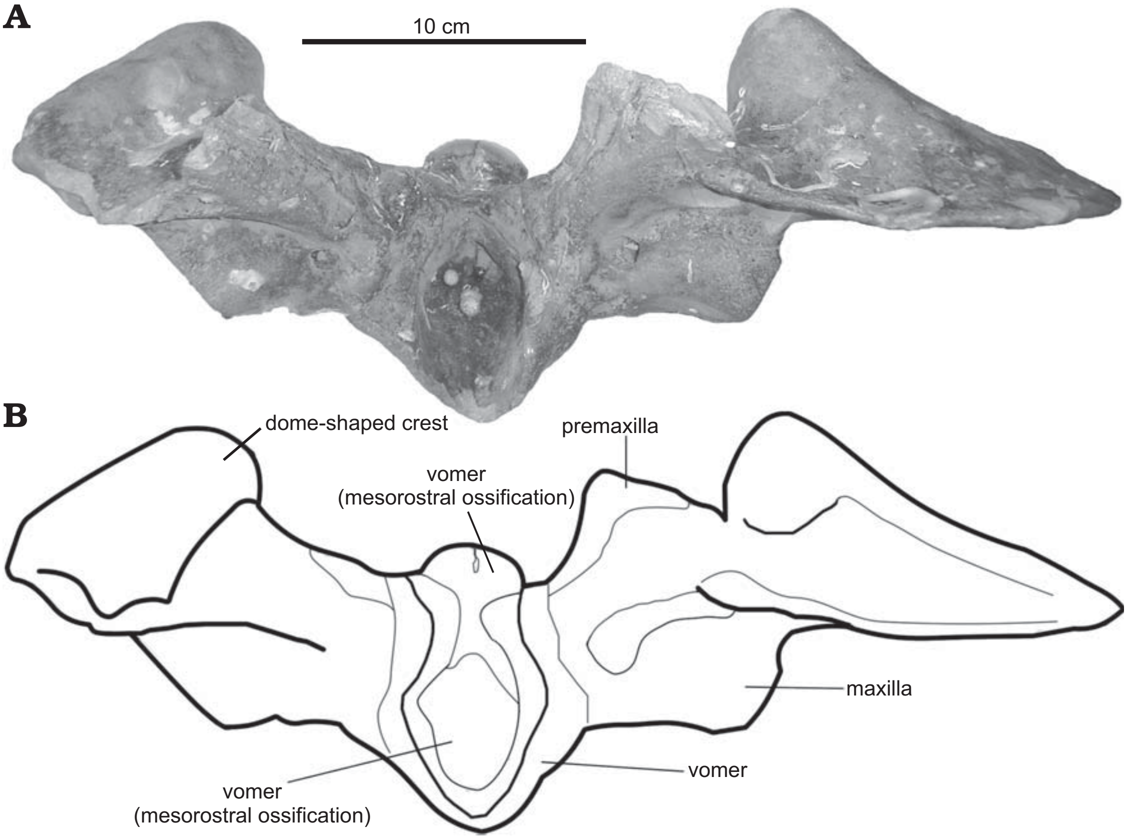

Fig. 4. The beaked whale *Africanacetus* sp., skull (YugNIRO 409) in posterior view. **A**. Photograph. **B**. Explanatory drawing.

the strengthening of the male rostrum for aggressive male-male interactions (Heyning 1984; MacLeod 2002). Unlike *Mesoplodon* and *Ziphius*, members of the extant genus *Hyperoodon* lack a mesorostral ossification, and instead are characterised by extremely high maxillary crests. In *H. ampullatus*, the crests are larger in males and vary in their development with age. By contrast, in *H. planifrons* the maxillary crests are underdeveloped even in adult males, although they are still higher than in *Mesoplodon*. Finally, apart from the mesorostral ossification and the development of bony crests, fusion of the premaxillae in some fossil ziphiids has been suggested as a third form of sexual dimorphism not seen in any extant species (Dooley 2010; Lambert et al. 2010).

Fig. 5. The beaked whale *Africanacetus* sp. (YugNIRO 408), narial region of the skull in ventral view.

Both a mesorostral ossification and high maxillary crests occur, and indeed are well developed, in the specimens of *Africanacetus* described here. While the mesorostral ossification of the latter resembles that of *Mesoplodon* and several extinct species in being formed by the vomer and bearing a median suture, it is more hypertrophied than in any of these taxa, except for the extinct *Mesoplodon tumidirostris* (see Miyazaki and Hasegawa 1992), very old individuals of *Ziphius cavirostris*, and some specimens of *Africanacetus ceratopsis* (e.g., SAM PQ 3002).

The bone histology of ziphiids with its complex pattern combining pachyosteosclerotic and osteoporotic structures (Lambert et al. 2011) has been interpreted as an expression of peramorphosis (Alberch et al. 1979; Ricqlès and Buffrénil 2001), with the hypertrophied mesorostral ossification being the result of hypermorphosis (Beer 1930), and the osteoporotic bone characterising other parts of the skeleton arising from predisplacement (“gerontomorphosis”). Peramorphosis has been specifically suggested for *Mesoplodon densirostris* (MacLeod and Herman 2004: 183), and the rostrum and facial skull of beaked whales show several additional traits which may also be peramorphic, such as fusion of the skull bones and bizarre bony structures (crests and swellings) developing in adulthood. Peramorphosis and hypermorphosis have been suggested to be the result of sexual selection in a

Fig. 6. Geographical range of the beaked whale *Africanacetus*. 1, type area; 2, Banzare Bank (from where the present material was recovered).

broad variety of animals (Gould 1977; Kelly and Adams 2010), and it is possible that the latter also drove the evolution of the hypertrophied mesorostral ossification and the overdeveloped maxillary crests of *Africanacetus*. In this case, the fossils from Banzare Bank whales might represent an overgrown descendant of *A. ceratopsis* from South Africa, although testing this hypothesis must await the discovery of further and better preserved specimens.

Geographical distribution.—The present material represents the southernmost record of any fossil beaked whale, replacing an earlier report of a partial skull photographed on the sea floor at 54°S, 150°E (Whitmore and Kaltenbach 2008: fig. 14). Our specimens were found in the sub-Antarctic region of the Indian Ocean, approximately 6,000 km from the South African type locality (Fig. 6), thus possibly indicating a circum-Antarctic distribution of *Africanacetus*. Interestingly, models describing the ranges of extant odontocetes predict their highest diversity in temperate waters of the Southern Hemisphere, with few species occurring in the sub-Antarctic region (Kaschner et al. 2011). As far as can be judged by the limited number of specimens available, and bearing in mind the caveat of potential sampling biases, this seems to be reflected in the distribution of fossil ziphiids: while the waters around South Africa have yielded a rich Neogene ziphiid fauna (Bianucci et al. 2007, 2008), the record of fossil ziphiids from the sub-Antarctic is relatively scarce.

A circum-Antarctic range is extremely common among extant ziphiids, and has been observed for all extant austral ziphiids except *Mesoplodon traversii*, for which the range is unknown (Rice 1998; MacLeod 2009). While many of these species are largely bound to either higher latitudes or more temperate waters, others (e.g., *Hyperoodon planifrons*) extend from polar to subtropical waters, thus covering both of the known localities of *Africanacetus* (Taylor et al. 2008). *Africanacetus* seems to have been relatively abundant, with 9 out of the 32 South African fossil ziphiid specimens reported by Bianucci et al. (2007) belonging to this genus, in addition to the two skulls reported in this study. Based on this, future discoveries of additional specimens of this genus from austral waters seem likely.

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