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Anatomical description and phylogenetic analysis of Miocene beaked whale from the East African Rift Valley, Kenya

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Abstract

This study compares the anatomy of a Miocene whale fossil found in Kenya to that of modern and other fossil beaked whales in order to identify it using phylogenetic analysis. The specimen is a partial skull and lacks diagnostic features present in the posterior regions of the skull, but a parsimony analysis based on available characters determined the whale is likely linked to modern *Mesoplodon* and *Hyperoodon*. Identification of this specimen is necessary for biogeographical purposes and other investigations using the fossil as a marker for the paleocoastline. Furthermore, this whale is an important and unique tool that can be used to study the development of the East African Rift.

Introduction

Beaked whales, members of the family Ziphiidae, are found in the cold waters from both poles of the Earth to the warm tropical waters at the Equator (MacLeod et al., 2006). Ziphiid diversity through time is reflected in the number of fossil cetacean genera throughout the Cenozoic portion of Earth's history and peaked in the middle Miocene, about 15 million years ago, with more than 75 genera (Uhen and Pyenson, 2007).

The 17 million year old fossil whale skull involved in this study was discovered in 1964 by Dr. James G. Mead in West Turkana, Kenya (35° 50' E, 02° 20' N) during an expedition led by Bryan Patterson (Mead, 1975). Dr. Mead originally studied the skull, and published his findings in 1975, after which the skull went missing until late 2011. Following its rediscovery, the specimen was scanned for this study at the University of Texas at Austin High Resolution CT Laboratory and the Southern Methodist University Visualization Laboratory using a NextEngine 3D laser surface scanner. Digital data were processed at SMU. The skull has since been returned to the National Museums of Kenya.

Containing 21 recognized extant species, Ziphiidae is the second most extensive family of the order Cetacea (MacLeod et al., 2003). However, this family remains one of the least understood (MacLeod, 2006). Several species are described by only a few specimens, and the availability of well-preserved specimens is limited (Lambert, 2005). Furthermore, 24 fossil beaked whale species have been defined with the possibility of this number increasing as more fossils are discovered (Bianucci et al., 2007).

Despite difficulties in identification and description, researchers have come to associate several characteristics with beaked whales. For example, the well-developed tusks of male whales are believed to be weapons used to fight other males for female partners (MacLeod, 2006). Scarring patterns found on modern beaked whales support a mode of combat similar to that of jousting (MacLeod, 2002).

Considered deep divers, some beaked whale species have been known to reach depths of 1800m where echolocation is necessary to detect prey (Lambert et al., 2011). Studies have shown that active sonar, specifically those associated with military exercises, can adversely affect this diving behavior and cause mass stranding events (Parsons et al., 2008).

The asymmetry present in toothed whale skulls has generally been attributed to the production of biosonar, but other studies have shown a possible link between the skull asymmetry and the asymmetrical positioning of the larynx which is believed to help these whales swallow larger prey (MacLeod et al., 2007). Beaked whales generally eat cephalopods and fish with lesser proportions of crustaceans; the diet can vary depending on the oceanic temperature and environment (MacLeod et al., 2003).

Materials and Methods

With a total length of 82cm, the Miocene beaked whale specimen seen in Fig. 1 is comprised of only the rostrum and portions of the skull anterior to the bony nares (Mead, 1975). The specimen contains grooves on the dorsal surface of the rostrum that appear to separate the maxillae, premaxillae, and vomer in the rostrum but become less visible as they extend posteriorly (Mead, 1975). Although the skull may have undergone some extent of compression during fossilization, it contains a pair of symmetrical elevations extending laterally from the premaxillae to the maxillae (Mead, 1975).

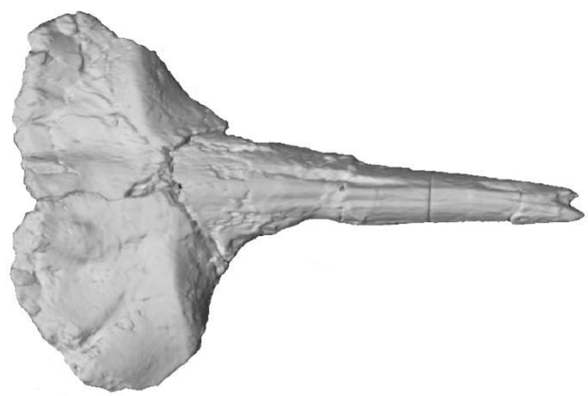


Fig. 1. – Quicktime rendering of the Miocene beaked whale fossil using CT data. Rendering was compiled by Michael Polcyn of the Visualization Laboratory at SMU.

All comparative specimens examined for this study are curated in the Smithsonian Institution's Marine Mammal Collection. During a five day period at the institution, a total of 36 extant and fossil beaked whale specimens were studied. Table 1 shows measurements of the skulls of modern whales taken using vernier calipers. Measurement guidelines from Bianucci et al. (2007) were used.

In addition, character traits were scored and described in accordance to Mead and Fordyce (2009) and phylogenetic matrices from Lambert (2005); field notes, containing personal observations and descriptions for individual specimens, are presented along with pictures. Due to the condition of the Miocene whale fossil from Kenya and its lack of posterior regions of the skull, the figures and descriptions provided in this report focus on the dorsal surface of the anterior skull and beak. Specimens that were too incomplete to apply to this comparison were not included.

Results

Measurements

	A	B	C	D	E	F	G	I	J	K	L
1	80.2cm	28.8(?)cm	48.2cm	41.8cm	86.2cm	-	50.5cm	45.0cm	40.9cm	51.3cm	42.0cm
2	80.2cm	20.6(?)cm	48.2cm	41.8cm	74.2cm	-	37.1cm	45.0cm	40.9cm	45.5cm	38.3cm
3	80.2cm	28.8(?)cm	48.2cm	41.8cm	86.2cm	-	50.5cm	45.0cm	40.9cm	51.3cm	42.0cm
4	14.5cm	107.99(?)	54.46	6.1cm	20.2cm	-	102.20	63.93	77.85	104.91	10.4cm
5	11.2cm	10.1(?)cm	64.92	63.73	9.7cm	-	71.16	45.12	50.38	63.74	11.5cm
6	3.1cm	17.67	11.72	12.72	29.26	-	26.71	10.60	27.18	34.66	53.52
7	27.1cm	19.0cm	10.5cm	9.9cm	36.5cm	34.3cm	23.7cm	14.5cm	16.0cm	23.7cm	24.0cm
8	36.0cm	22.9cm	21.7cm	18.3cm	44.3cm	42.6cm	27.5cm	22.4cm	23.1cm	31.9cm	31.9cm
9	110.82	90.58	4.5cm	34.38	118.64	-	68.93	47.14	54.30	82.88	7.7cm
10	167.3cm	143.96	11.3cm	93.66	22.9cm	24.4cm	12.5cm	109.18	113.99	17.3cm	20.2cm
11	77.60	54.52	50.95	41.18	9.5cm	120.17	70.75	51.35	57.19	102.24	8.3cm
12	59.26	44.20	36.82	36.16	8.2cm	96.31	28.92	38.06	43.22	44.98	6.2cm
13	84.30	66.87	51.31	43.04	100.34	94.19	77.16	52.82	56.08	72.73	9.7cm
14	33.87(L) 39.72(R)	25.81(L) 43.43(R)	22.96(L) 36.40(R)	19.03(L) 28.88(R)	44.86(L) 52.94(R)	39.46(L) 47.91(R)	29.97(L) 43.00(R)	22.62(L) 33.73(R)	24.34(L) 32.94(R)	31.34(L) 77.93(R)	1.7(L)cm 4.1(R)cm
15	18.2cm	17.9cm	14.7cm	129.77	20.4cm	20.0cm	25.5cm	15.8cm	15.7cm	17.3cm	20.1cm
16	69.41	94.19	91.62	73.13	50.65	52.82	10.4cm	83.34	79.86	7.3cm	6.8cm
17	58.84	52.55	68.03	57.69	37.05	38.19	5.5cm	56.04	64.11	45.12	4.6cm
18	53.08	39.93	17.32	6.07	106.51	105.19	9.4cm	23.14	18.83	59.39	7.9cm
19	92.18	67.97	34.41	31.81	125.34	126.71	7.6 cm	40.42	41.94	77.39	8.2cm
20	94.09	44.01	15.98	12.49	132.04	94.70	5.62	25.29	14.14	103.01	9.8cm
21	57.03	74.31	56.11	63.49	132.97	132.53	8.5cm	37.11	43.37	76.96	65.01
22	13.0cm	5.1cm	72.67	63.73	15.0cm	-	11.7cm	76.49	66.76	7.2cm	13.2cm
23	20.2cm	10.6cm	52.84	6.1cm	24.6cm	-	13.3cm	77.28	76.49	16.5(v)cm	21.8(v)cm

Table 1. – Measurements of extant beaked whale skulls.

All measurements in (mm) unless otherwise noted. Abbreviations: e, estimate; -, no data. A – *Tasmacetus shepherdi*, USNM484878; B – *Indopacetus sp*, USNM593534; C – *Mesoplodon densirostris*, USNM550952; D – *M. densirostris*, USNM504950; E – *Berardius bairdii*, USNM571529; F – *B. bairdii*, USNM571527; G – *Hyperoodon ampullatus*, USNM14449; H – *Mesoplodon europaeus*, USNM504256; I – *M. europaeus*, USNM360854; J – *Ziphius cavirostris*, USNM504938; K – *Z. cavirostris*, USNM504940.

1. Length of rostrum	9. Maximum premaxillary width on rostrum	17. Width of left premaxillary crest
2. Length of maxilla on rostrum	10. Width of premaxillary sac fossae	18. Minimum distance between premaxillary crests
3. Length of premaxillary portion of rostrum	11. Width of right premaxillary sac fossa	19. Maximum width of nasals
4. Width of rostrum at mid-length	12. Width of left premaxillary sac fossa	20. Length of medial suture of nasals on vertex
5. Height of rostrum at mid-length	13. Width of bony nares	21. Minimum posterior distance between maxilla
6. Maximum opening of mesorostral groove	14. Minimum width of ascending process of premaxilla	22. Maximal anterior height rostrum
7. Width of rostrum base at prominental notch	15. Width of premaxillary crests	23. Maximal anterior width of rostrum
8. Width of rostrum base at antorbital notch	16. Width of right premaxillary crest	Measurement guidelines from Bianucci et al. (2007).

Table 2. – List of measurements taken.

Measurement guidelines from Bianucci et al. (2007).

Descriptions

Fig. 2: *Choneziphius liops* – USNM11718

The maxillary foramens appear to be more anteriorly and laterally skewed. In particular, one opening is just anterior of the antorbital notches. Other holes are laterally organized on the rostrum and are symmetrical on both lateral sides of the rostrum. The premaxilla extends laterally over the maxilla. The skull may have been anteriorly-posteriorly compacted because the bony nares are almost at the same anterior-posterior location as the antorbital notches. The rostrum is broken off and therefore no definitive measurement of full length or orientation can be obtained. However, it is apparent that the more posterior regions of the rostrum diverge toward the antorbital notches. The premaxillae appear to fuse and form a roofing over the anterior region of the rostrum. Prominental notches appear to be missing as only the anteorbital notches are readily visible.

Measurements: 8. 145.64mm, 10. 140.80mm, 11. 81.57mm, 12. 48.15mm

Fig. 2. – Dorsal view of *Choneziphius liops* – USNM11718. Scale bar = 10cm.

Fig. 3: *Choneziphius trachops* – PAL534027 (Cast)

A void or canal through middle of the rostrum is visible. The premaxilla meets at the dorsal region and forms a roofing. The widest and highest portion of the rostrum are roughly at the middle length. The prenarial region – most likely premaxilla – slopes upward. No bulbous ossification like that seen in male *Ziphius carvirostris* is present. The antorbital notches cannot be seen, nor are there defined prominental notches. The palatine appears to be well developed, stretching medially to the most anterior tip of the rostrum.

Fig. 3. – Dorsal view of cast of rostrum. *Choneziphius trachops* – PAL534027. Scale bar = 10cm.

Fig. 4: *Choneziphius liops* – USNM5548

The foramen on the lateral edge of the maxilla are likely not as lateral as they appear. This is because on the left lateral side, the lacrimal foramen is more dorsally oriented than it is on the right lateral side – that is, you cannot see the opening from the right side. The vomer and premaxilla sutures are difficult to follow. It appears that the premaxillae do not meet in the anterior portion of the rostrum to form a roofing. However, with the state of preservation, it is, admittedly, hard to tell. Mesorostral ossification is similar to that of *Z. cavirostris*. The extensive ossification leads to a skewing of the rostrum to one side. This asymmetry could have been amplified by burial compression. There are depressions near where the grooves of the premaxillae disappear as they meet the maxillae and vomer.

Fig. 4. – Dorsal view of *Choneziphius liops* – USNM5548.

Fig. 5: *Choneziphius trachops* – USNM186793

The premaxillae meet and form a roofing anteriorly on the rostrum; this roofing encloses a tube or void in the specimen and creates a sort of bulge which appears heavily ossified. Grooves, perhaps indicating bone sutures, can be seen from lateral view separating premaxillae and maxillae. From the ventral view, supraoccipital and palatine form a junction along the medial line which runs into the medial suture that stretches to the most anterior tip of rostrum. There are symmetrical foramens at proposed premaxillary and maxillary contact near the rostrum base.

Measurements: 6. 20.16mm, 9. 50.04mm, 22. 77.51mm, 29. 83.73mm.

Fig. 5. – Dorsal view of rostrum. *Choneziphius trachops* – USNM186793. Scale bar = 10cm.

Fig. 6: *Proroziphius chonops* – USNM16689

There are foramens on the maxilla at the premaxillary-maxillary junction near the rostrum base. The mesethmoid extends to the middle of the rostrum. The rostrum has a canal, and the premaxillae appear to join and form a dorsal roofing at an elevated section on the rostrum. However, this character is difficult to determine as the more anterior region of the rostrum was not preserved. The ventral surface contains a pointed bump anterior to the rostrum base at the location of the maximum height of the rostrum.

Fig. 6. – Dorsal view of rostrum. *Proroziphius chonops* – USNM16689. Scale bare = 10cm.

Fig. 7: *Mesoplodon planirostris* – USNM453050

This specimen contains only the beak and anterior portion of the skull. Lateral portions, including the maxillary crest, were not preserved. Two foramens near the rostrum base are readily visible from the dorsal view. Suture lines are present but faint and suggest the premaxillae do not meet to form a roofing. Instead, the vomer appears to be developed and is present at or above the elevation of the bordering premaxillae throughout the rostrum. The ventral side of the beak has a streamlined shape and is rounded laterally. It is difficult to tell from this specimen if the lateral portions of the rostrum extend towards the antorbital notches as these features are not preserved in the fossil.

Fig. 7. – Dorsal view of rostrum. *Mesoplodon planirostris* – USNM453050. Scale bare = 10cm.

Fig. 8: *Tasmacetus shepherdi* – USNM484878

One of the larger specimens examined in this study, this adult female *T. shepherdi* has rounded elevations on the maxillary crests just posterior to the rostrum base. These rounded elevations are similar to those found on the fossil skull from Kenya. The premaxillae do not meet on the dorsal surface of the rostrum. It appears that the mesethmoid of this specimen is broken off and could have extended further anteriorly; the development of the vomer causes this skull to have a more v-shaped section at the base of the rostrum (Lambert et al., 2011). The rostrum diverges toward the antorbital notches in the more posterior sections of the beak.

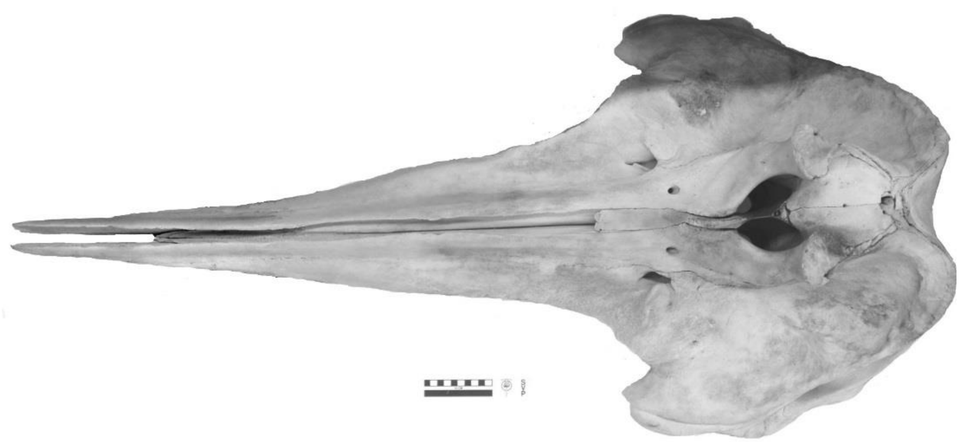
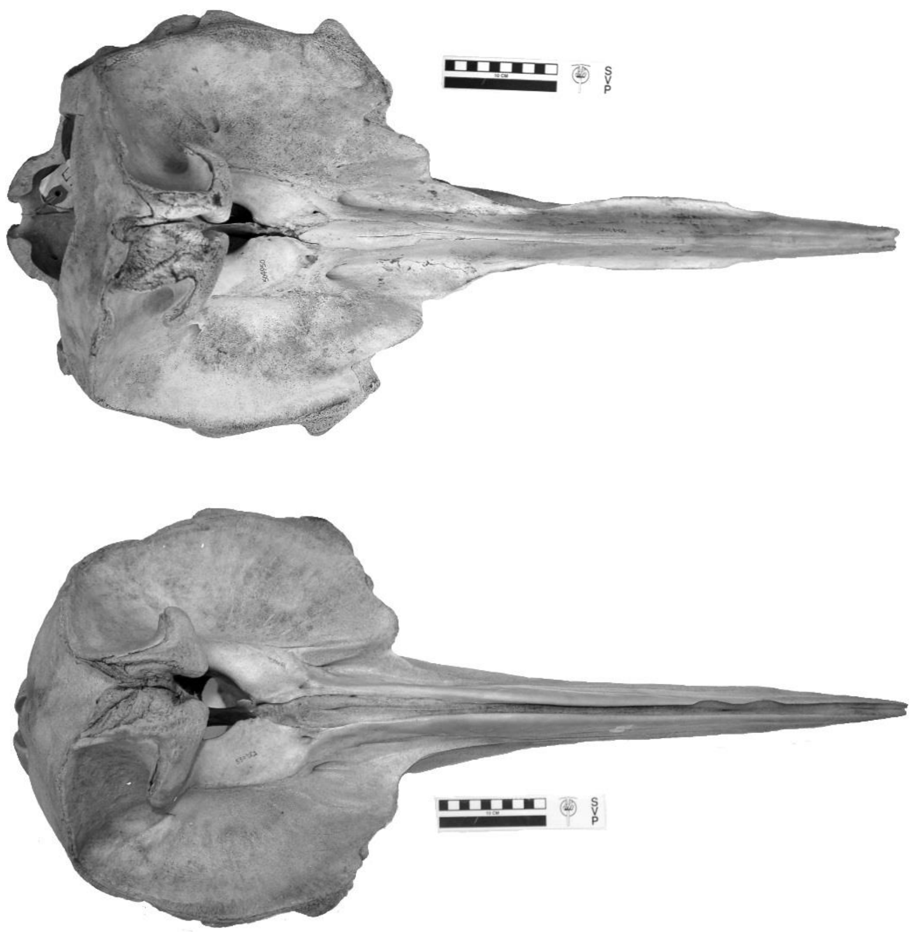


Fig. 8. – Dorsal view of *Tasmacetus shepherdi* – USNM484878. Scale bar = 10cm.

Fig. 9: *Mesoplodon densirostris* – USNM504950, USNM550952

A male (USNM504950, Fig. 8a) and a female (USNM550952, Fig. 8b) *Mesoplodon densirostris* were examined in this investigation. Both share an elongate rostrum that diverges toward the antorbital notches near the rostrum base. The vomer is more prominent from the dorsal view on the male specimen than on the female one. While the margins at the middle of the rostrum on the male specimen expands laterally, the margins on the female rostrum do not. The premaxillae of the specimens do not meet on the dorsal face of the rostrum. Both skulls exhibited high rostral density; most of the weight was concentrated in the beaks.



(A)

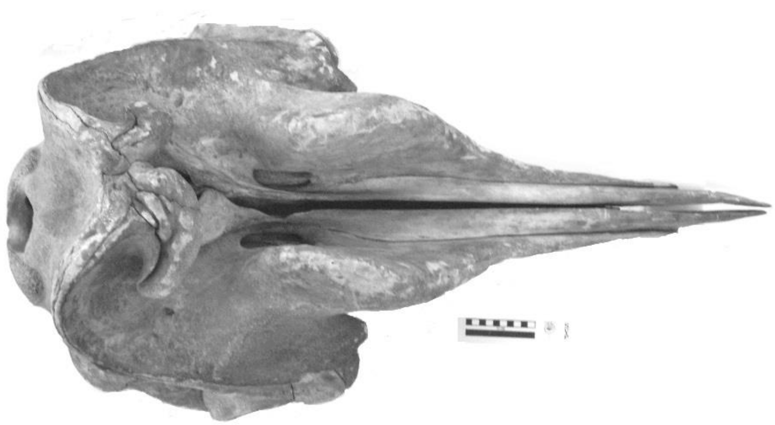
(B)

Fig. 9. – A. *Mesoplodon densirostris* USNM504950; B. USNM550952. Scale bare = 10cm.

Fig. 10: *Hyperoodon ampullatus* – USNM14449

This specimen has enlarged maxillary crests on the rostrum which is a characteristic limited to male *Hyperoodon* (Lambert et al., 2011). As these crests extend laterally and upward, they are best seen from the lateral view in Fig. 6a. No such structures appear to be associated with the Miocene beaked whale fossil from Kenya. The premaxillae, bordered by the maxillae through the entire length of the rostrum, do not meet dorsally to form a roofing. Mesorostral ossification is not elevated above the level of the premaxillae. Asymmetry in the size of the premaxillary sac fossa is apparent. The posterior region of the rostrum diverges laterally, but the presence of the enlarged sections of maxillary bone may contribute to this appearance.

(A)



(B)

Fig. 10. – *H. ampullatus* USNM14449; A. Right lateral view; B. Dorsal view. Scale bars = 10cm.

Fig. 11: *Ziphius cavirostris* – USNM504938, USNM504940

The *Z. cavirostris* specimen, USNM504938 (Fig. 10a), is female while USNM504940 (Fig. 10b) is male. Both skulls have similar rostral shapes and orientations. The divergence of the posterior portion of the rostrum is accomplished gradually and begins at the most anterior portion of the beak. The premaxillary sac fossae on both specimens exhibit high degrees of asymmetry; the right lateral sac fossa is much larger than the left lateral one. The premaxillary sac fossae also contain portions that are hanging over the maxillae. Prenarial basin is present; this character has been associated with *Z. cavirostris* (Mead and Fordyce, 2009). The male skull, as shown in Fig. 10b, shows a bulbous ossification in the middle portion of its rostrum; this ossification is lacking in the female specimen.

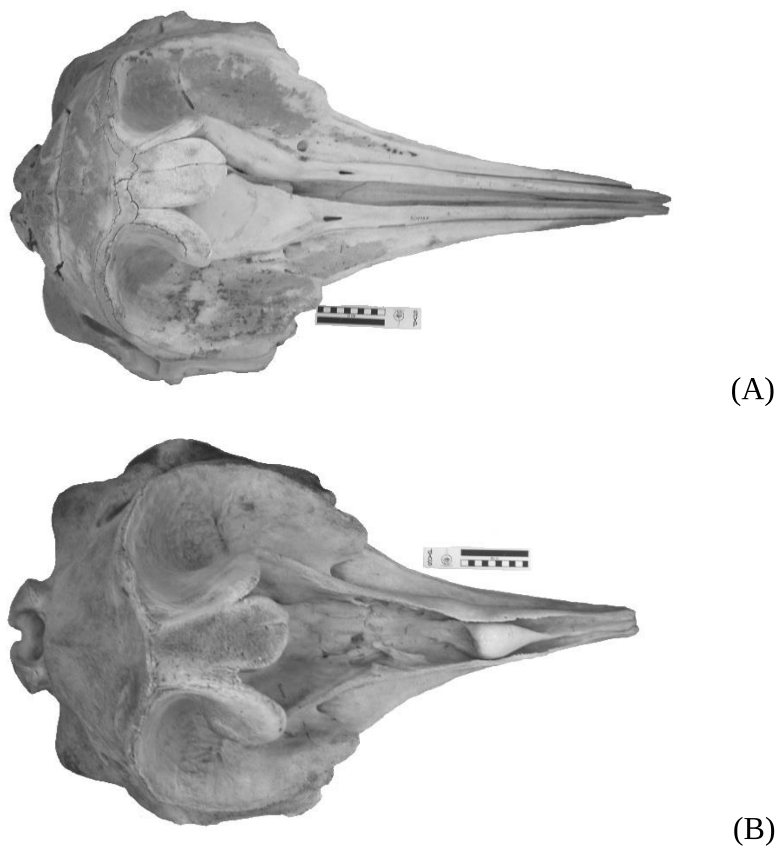


Fig. 11. – A. Dorsal view of *Z. cavirostris* skull, USNM504938; B. Dorsal view of *Z. cavirostris* skull, USNM504940. Scale bar = 10cm.

Conclusion

Though poorly preserved and lacking major diagnostic regions of the skull, this specimen found in Kenya can be readily described as a beaked whale due to its prolonged rostrum and reduced dentition – both qualities indicative of the family Ziphiidae (Mead, 1975). To conduct a phylogenetic analysis of this beaked whale, the character matrix found in Lambert (2005) was utilized as a baseline. The observations and measurements acquired at the Smithsonian Institution served to improve the assignment of character scores to the Miocene whale.

To carry out the phylogenetic analysis, the program TNT was used to run a phylogenetic tree search based on parsimony (Goloboff et. al, 2008). The matrix used included all the taxa from Lambert (2005) as well as the fossil whale from Kenya. Due to the limitations of the fossil, some characters were scored as missing.

The presence and orientation of the mesorostral ossification and the bordering premaxillae, divergence of the rostrum at the rostrum base, and lack of prenarial basin all suggest a possible link between the fossil whale and modern *Mesoplodon* and *Hyperoodon*. Two of the resulting cladograms seen in Fig. 12 reflect this relationship as do the original findings by Mead (1975). Though Mead suggests the fossil whale was more closely related to other Miocene genera, *Belemnoziphius* and *Proroziphius*, modern *Mesoplodon* and *Hyperoodon* were likely derived from these earlier genera (Mead, 1975).

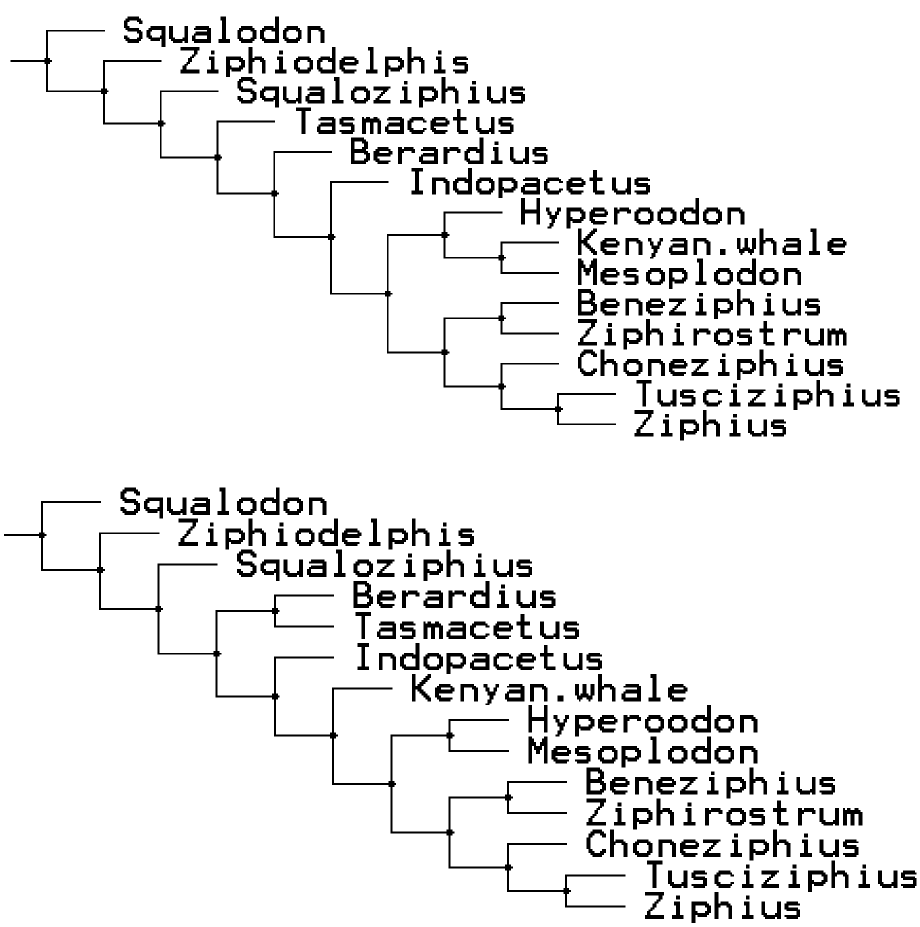


Fig. 12. – Two of the resulting phylogenetic trees from analysis of the Lambert (2005) matrix and the fossil beaked whale from Kenya.

This specimen, the beak and anterior portion of the skull, is particularly valuable as it was found associated with sediment containing fauna suggesting a freshwater-terrestrial environment (Mead, 1975). While the whale could have mistakenly swum into freshwater from its more natural marine habitat (Mead, 1975), its location can still be helpful in determining the paleocoastline. This study has helped to support the identification of the specimen as a beaked whale, and this fossil can now be used in other studies relating to geophysical reconstructions of the region.

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