

APPEARANCE, DISTRIBUTION, AND GENETIC
DISTINCTIVENESS OF LONGMAN'S BEAKED
WHALE, *INDOPACETUS PACIFICUS*

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ABSTRACT

Longman's beaked whale, *Indopacetus pacificus*, was known previously from only two skulls. Here we describe four new specimens of this species from strandings in the western and central Indian Ocean. Two juveniles, previously misidentified from external morphology as *Hyperoodon planifrons*, were identified as *I. pacificus* through diagnostic characteristics of mitochondrial (mt) DNA sequences derived from the holotype of this species. Images of the external appearance and teeth of the species are presented for the first time. Comparison of the color pattern of these new specimens with that of "tropical bottlenose whales" sighted in the tropical Indian and Pacific oceans confirm that those unidentified whales represent *I. pacificus*. Moore (1968) erected a new genus, *Indopacetus*, for this species (described initially as *Mesoplodon pacificus*) based primarily on cranial morphology. Phylogenetic analyses of short mtDNA fragments available from the specimens known to date were unable to resolve the validity of this genus. However, the diagnostic osteological features highlighted by Moore (1968) for *Indopacetus* were also observed in the new specimens. Rib count and number of fused cervical vertebrae may also be diagnostic. Rostrum depth at mid-length and melon shape further distinguish this species from *Mesoplodon* beaked whales. As such, we see no reason on morphological grounds to overturn Moore's (1968) proposal that Longman's beaked whale is sufficiently distinct to be afforded its own genus.

Key words: molecular genetics, mtDNA, holotype, species identification, taxonomy, external appearance, osteology, distribution, tropical bottlenose whales.

Longman's beaked whale, *Indopacetus pacificus*, is considered one of the rarest of all cetaceans (Jefferson *et al.* 1993, Rice 1998). Only two specimens have been described to date: the holotype, a skull and mandible found beachcast at Mackay, northern Queensland, Australia in 1882 (*Mesoplodon pacificus*; Longman 1926), and a second skull and mandible found in a fertilizer factory in Danane, Somalia, in 1955 (Azzaroli 1968). Based on the holotype, Raven (1937) suggested that Longman's beaked whale was simply a larger Pacific form of True's beaked whale, *M. mirus*. McCann (1962c) disagreed and suggested instead that it represented the damaged skull of a female southern bottlenose whale, *Hyperoodon planifrons*. The discovery of the second specimen and a series of comprehensive morphological evaluations by Moore (1957, 1968, 1972) refuted both hypotheses and confirmed the morphological distinctiveness of the species. Moore (1968) also suggested that Longman's beaked whale was sufficiently distinct from other ziphiid taxa to warrant the erection of a new genus, *Indopacetus*. Although accepted by some (*e.g.*, Rice 1998), the validity of this genus is still in debate (*e.g.*, Mead 1989a).

The external appearance of Longman's beaked whale remained unknown. Skull morphology and the original classification (Longman 1926) suggest that it may resemble a large beaked whale of the genus *Mesoplodon* (*i.e.*, with a spindle-shaped body, a small head in relation to the thorax and abdomen, and without a distinct notch between the rostrum and gently sloping melon; Mead 1989a). Calculations based on skull dimensions indicate that the holotype (considered to be an adult male by Moore 1968) was ~7 m in length (Pitman *et al.* 1999), slightly larger than *Mesoplodon* spp. Mörzer Bruyns (1971) suggested that unidentified "very large beaked whales" observed in the warmer waters of the Indian and Pacific oceans could be Longman's beaked whales. Whales similar to those he described have been sighted subsequently. They are similar in general body form and color pattern to

southern bottlenose whales, *H. planifrons*, with an estimated adult length of 7–8 m (Pitman *et al.* 1999) and have been referred to as “tropical bottlenose whales.” Melon shape is variable; larger than in *Berardius*, but less pronounced and bulbous than in *Hyperoodon* (Pitman *et al.* 1999). Analyses of size, scarring patterns, and distribution of sightings have provided additional support for the hypothesis that Longman's beaked whale and tropical bottlenose whales are one and the same (Ballance and Pitman 1998, Pitman *et al.* 1999).

Here we present information on four new specimens of Longman's beaked whale: two juvenile males stranded on the Indian Ocean coast of South Africa, an adult female stranded in the Republic of Maldives, and the skull of an adult assumed from its provenance to be from Kenya. The two juvenile specimens were initially misidentified as southern bottlenose whales *H. planifrons* from external morphology; one was described in some detail by Ross (1984). These specimens are here identified as *I. pacificus* through phylogenetic comparisons to a comprehensive DNA reference database for beaked whales (Dalebout 2002). The Maldivian specimen was identified as *I. pacificus* from external and skull morphology, and its species identity confirmed through genetic analyses. The new Kenyan skull was identified as *I. pacificus* based on morphology alone. This paper includes a genetic description of Longman's beaked whale, as well as discussion of the distribution, external appearance, and taxonomy of this species.

METHODS

Material Examined

Six specimens were examined. Numbers 1–2 were described previously, whereas numbers 3–6 are new specimens.

1. Skull and mandible (QM-J2016) held at the Queensland Museum, Brisbane, Australia. Collected in 1882 by E. W. Rawson from Mackay, Queensland, Australia (21°10'S, 149°10'E). Holotype of *Indopacetus pacificus*. Described and named (*Mesoplodon pacificus*) by H. A. Longman in 1926. Considered likely to represent an adult male (Moore 1968).

2. Skull and mandible (MZUF 1956 [M4854]) held at the Natural History Museum, Zoological Section 'La Specola' at the University of Florence, Italy. This whale was found stranded near Danane, Somalia (1°52'N, 45°02'E) by local fishermen in 1955 and taken to a nearby fertilizer factory for oil extraction and use as organic fertilizer.² Skull and mandible described by Azzaroli (1968). Considered to represent a possible subadult female based on skull size and proportions in comparison to the holotype (Azzaroli 1968, Moore 1972).

3. Skull without mandible (OM7622) held at the National Museum of Kenya, Nairobi, Kenya. Discovered at the International School of Kenya, Nairobi, Kenya by H. L. Hinsz. Collected from an unknown location on the Kenya coast *ca.* 1968 (based on accounts from long-time workers at the school, which was moved to Nairobi in 1968, who remember this distinctive large skull as one of two skulls which framed the wall where movies were shown). Sex unknown.

4. Several ribs and vertebrae (PEM292) held at the Port Elizabeth Museum, South Africa. Complete specimen collected by G. J. B. Ross from Blythesdale Beach,

² Personal communication from P. Agnelli and U. Funaioli, Natural History Museum 'La Specola', University of Florence, Italy, e-mail, 23 October 2001.

Natal, South Africa (29°39'S, 31°36'E) on 7 November 1976. Total length of specimen, 291 cm. Juvenile male (neonate). Collected by G. Thurmer, and dissected and described by Ross (1984) as *Hyperoodon planifrons* (original specimen code, PEM1520/30). Photographs were taken of the external appearance of this specimen when fresh and a detailed necropsy was performed on the body posterior to the head. However, the head was inadvertently disposed of following a freezer failure.

5. Skull, mandible, teeth, earbones, and ribs (PEM1960) held at the Port Elizabeth Museum, South Africa (registered as *H. planifrons*). Complete specimen collected by V. G. Cockcroft and V. Peddemors from Sodwana Bay, Natal, South Africa (27°34'S, 32°41'E) on 5 August 1992, with help from the staff of the KwaZulu-Natal Nature Conservation Services (formerly Natal Parks Board) and the Natal Sharks Board. Juvenile male. Total length of specimen, 363 cm.

6. Skull, mandible, teeth, and postcranial material (no reference number) held at the Marine Research Centre, Ministry of Fisheries, Agriculture and Marine Resources, Malé, Republic of Maldives. Complete specimen (including the remains of a 104-cm long fetus) collected from Felidhu Atoll, Republic of Maldives (3°26'N, 73°26'E) on 17 January 2000, by R. C. Anderson with help from the staff of the Marine Research Centre. Adult female. Total length of specimen (curvilinear), 596 cm. The skeletal material obtained from this specimen will be transferred to a dedicated display hall in the Republic of Maldives in due course.

The comparative rarity of beaked whales and their often non-distinct morphological features are a general problem with the identification of species in this group. To assist in species identification, a DNA reference database of mitochondrial (mt) DNA control region and cytochrome *b* sequences has been compiled for all 21 described species of beaked whales (Dalebout 2002). All specimens in this database, which includes the holotype of Longman's beaked whale (QM-J2106), are validated by diagnostic skeletal material or photographic records held in museums and archives. Through phylogenetic comparisons to such a reference database, the species identity of unknown "test" specimens can be determined (*e.g.*, Henshaw *et al.* 1997, Dalebout *et al.* 1998). Using this database, phylogenetic analyses were used to confirm the identity of three of the four new Longman's beaked whales. To date, the Kenyan specimen has not been sampled for genetic analysis due to logistical difficulties.

Morphological comparisons were made to other ziphiid species. External measurements were taken following Norris (1961) for the two South African juveniles (PEM292 and PEM1960) by Ross and Cockcroft, respectively, and for the Maldivian adult female by Anderson. Cranial measurements and mandibular measurements following Moore (1972), were taken for specimens from Queensland, Somalia, Kenya, the Maldives, and South Africa (PEM1960) by several authors, together with limited information on tooth dimensions (see Tables 3 and 4 for details).

DNA Extraction and Sequencing

A hand-held electric drill with a 2-mm diameter drill bit was used to obtain 0.01–0.02 g of bone or tooth powder from each specimen. The drill site was cleaned with 70% ethanol to remove dust and particulate matter prior to drilling (see Pichler *et al.* 2001 for further information). The silica-based method of Höss and Pääbo (1993) was used to extract DNA from this material, with the addition of a proteinase-K digestion step at the beginning of the procedure to increase yields (Matisoo-Smith *et al.* 1997). Previously, these methods had been used to extract

DNA from bone powder from the holotype specimen. In addition, the Chelex method (Walsh *et al.* 1991) as modified by Baker *et al.* (1996) was used to extract DNA from degraded soft tissue from the Maldivian specimen and from the fetus that it carried. Given the non-recombining, maternal mode of inheritance of the mitochondrial genome (*e.g.*, Wilson *et al.* 1985), the Maldivian specimen and her fetus were treated as a single individual in these analyses.

Using the Polymerase Chain Reaction (PCR), short segments of the 5' end of the mtDNA control region and 5' end of the cytochrome *b* gene were amplified from all five specimens (see Appendix for primer sequences and further information). Sequences from these specimens were aligned by eye to the reference sequences comprising the beaked whale reference database (Dalebout 2002). These sequences have been submitted to Genbank (Accession Nos: AY162435–AY162444). The aligned reference sequence files and further information regarding reference specimens are available from the website <http://www.dna-surveillance.auckland.ac.nz>.

Phylogenetic Analyses

Phylogenetic relationships among the mtDNA control region and cytochrome *b* sequences from the new "test" specimens, the Somali specimen (MZUF 1956), and reference sequences from all 21 described beaked whale species in the database (including the holotype of *I. pacificus*) were reconstructed using neighbor-joining (NJ), maximum parsimony (MP), and maximum likelihood (ML) methods. For each locus, the length of the multiple sequence alignment used was set by the longest putative *I. pacificus* sequence available. The robustness of the resulting trees was evaluated by bootstrap resampling of the data. Baird's beaked whale, *B. bairdii*, was used as an outgroup as it likely represents the basal genus in this family (*e.g.*, Dalebout *et al.* 1998). Inclusion of more distant outgroup taxa (*i.e.*, representatives from other cetacean families) did not affect the branching patterns at any of the nodes relevant to this paper (Dalebout 2002). All phylogenetic analyses were conducted using the program PAUP* 4.0b10 (Swofford 1999). See Appendix for details of analysis parameters and settings.

RESULTS

DNA Sequence Data

Fragments of the mtDNA control region ranging in length from 226 to 409 base pairs (bp) and fragments of the cytochrome *b* ranging in length from 130 to 289 bp were sequenced successfully from all five specimens available for genetic analysis (Table 1). Attempts to amplify longer sequence fragments were unsuccessful, as expected from DNA extractions from bone, tooth, or degraded soft tissue (*e.g.*, Höss and Pääbo 1993). The DNA sequences obtained from the tooth of the Maldivian female and the soft tissue from her fetus were identical over the segment represented for both. Attempts to amplify these short mtDNA fragments from the decomposed soft tissue of the Maldivian female were unsuccessful. As slightly longer sequences were obtained from the fetal material, only these were included in the analyses.

Molecular Genetic Species Identification

In phylogenetic analyses of mtDNA control region (415 bp alignment) and cytochrome *b* (268 bp alignment) sequences, the Somali specimen (Azzaroli 1968),

Table 1. Sequence length and Genbank Accession Numbers for Longman's beaked whale mitochondrial DNA sequences used in this study. bp, base pairs; Seq, sequence. See Appendix for primer sequences.

Specimen	Control region			Cytochrome <i>b</i>			Reference
	Seq. length (bp)	Primers used	Accession No.	Seq. length (bp)	Primers used	Accession No.	
QM-J2016 ^a	244	Dlp10-L-Dlp4-H	AY162435	187	CYBMF-L-CYBMR-H	AY162440	Dalebout (2002)
MZUF 1956	409	M13-Dlp1.5-L-Dlp5-H	AY162436	187	CYBMF-L-CYBMR-H	AY162441	<i>this paper</i>
PEM292	295	M13-Dlp1.5-L-Dlp4-H	AY162437	268	CB1-L-CB2-H	AY162442	<i>this paper</i>
PEM1960	295	M13-Dlp1.5-L-Dlp4-H	AY162438	192	CYBMF-L-CYBMR-H	AY162443	<i>this paper</i>
Republic of Maldives	226	Dlp10-L-Dlp4-H	AY162439	130	CYBMF-L-CYBMR-H	AY162444	<i>this paper</i>

^a holotype.

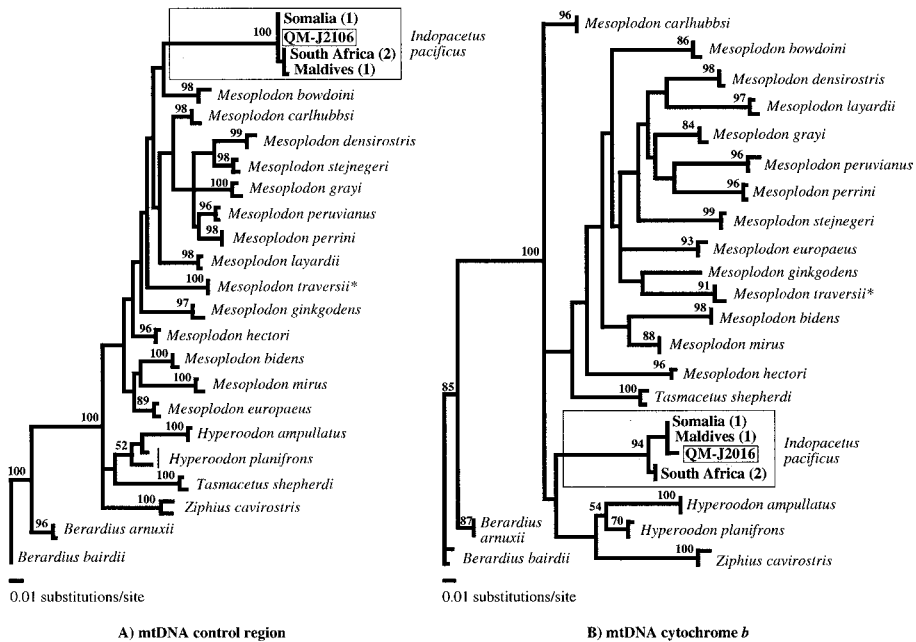


Figure 1. Phylogenetic relationships among the 21 described species of beaked whales (Ziphiidae) reconstructed using ML methods, based on A) a 415 bp alignment of mtDNA control region sequences and, B) a 268 bp alignment of mtDNA cytochrome *b* sequences. Nos. above internal nodes indicate bootstrap values >50% from 200 ML resamplings of these data. All species are represented by two reference specimens where possible. In each figure, the gray box highlights the specimens of Longman's beaked whale, within which the white box highlights the holotype. **Mesoplodon traversii* = *M. bahamondi*; see van Helden *et al.* 2002 for details.

and the three new specimens from South Africa and the Maldives grouped closely with the holotype of Longman's beaked whale confirming that all five animals represented the same species (ML bootstrap scores—control region, 100%; cytochrome *b* 94%; Fig. 1). The MP and NJ trees did not differ significantly from the ML trees shown at nodes relevant to this paper. All species-specific groupings were supported by high bootstrap scores (>80%). Southern bottlenose whales, *H. planifrons*, were the exception to this trend due to a deep intraspecific divergence at these genes (Dalebout 2002). Although well suited to species identification, these short mtDNA sequences did not yield robust reconstructions of higher-level relationships among the Ziphiidae (*i.e.*, most internal nodes were very short, with bootstrap scores <50%). Thus, no conclusions can be drawn from these trees about the validity of the genus *Indopacetus*. Note that while the genus *Mesoplodon* does not form a monophyletic clade in the cytochrome *b* tree (Fig. 1B), nor was monophyly strongly supported by the control region tree (where Longman's beaked whale branches among the *Mesoplodon* spp.; Fig. 1A), robust phylogenetic reconstructions based on long sequences from more slowly evolving single copy nuclear loci (missing Longman's beaked whale) support the validity of this genus (Dalebout 2002).

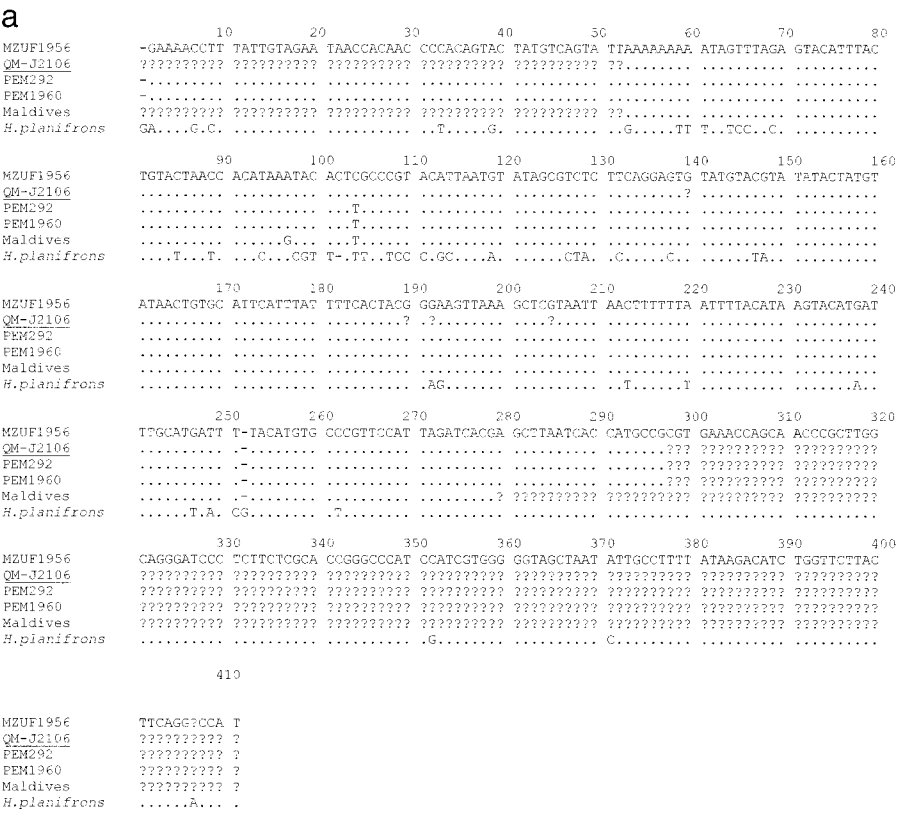


Figure 2. (a) Aligned mitochondrial DNA control region, and (b) cytochrome *b* sequences for five of the six known specimens of Longman's beaked whale, labeled as in Table 1. Identity to the top sequence is indicated by dots. Position 1 of the control region alignment corresponds to first nucleotide of this locus, and to position 15891 of the fin whale *Balaenoptera physalus* mtDNA genome (Arnason *et al.* 1991). Position 1 of the cytochrome *b* alignment corresponds to the 15th nucleotide (third position) of the cytochrome *b* gene, and to position 14627 of the fin whale mtDNA genome (Arnason *et al.* 1991). Sequences from the morphologically similar southern bottlenose whale *H. planifrons* (AUNZ Hpl01) are included in both alignments for comparison. Dash, nucleotide deletion; question mark, missing data.

Intra- and Interspecific Divergence

At the mtDNA control region, the holotype (QM-J2106) and the Somali specimen (MZUF 1956) shared the same haplotype and differed by one transition substitution from the shared haplotype of the two South African specimens (PEM292 and PEM1960). The haplotype represented by the Maldivian specimen differed by one transition substitution from the haplotype of the South African specimens (Fig. 2a). Over the maximum sequence length available (409 bp; MZUF 1956 [415 bp as aligned to other ziphiid species]), which covers the most variable portion of the ziphiid control region (Dalebout 2002), *I. pacificus* differed from all other beaked whales by an average of 11.01% (range: 8.68%, from Hector's beaked

b

	10	20	30	40	50	60	70	80
MZUF1956	AAAAACACAC	CGACTAATAA	AAATATACAA	TAATGCATTC	ATTGACCTCC	GAATCCGATC	AAACATCTCC	TCATGATGAA
QM-J2106
PEM292	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
PEM1960	??	??	??	??	??	??	??	??
Maldives	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
<i>H. planifrons</i>C.....C.....C.....C.....C.....C.....C.....C.....
	90	100	110	120	130	140	150	160
MZUF1956	ATTTCGGTTC	CCTACTCGGT	CTCTGCCTAA	TTATACAAAT	CCTTACAGGC	CTATTTCTAG	CAATACACTA	CACACCAGAC
QM-J2106
PEM292	?	?	?	?	T.....
PEM1960	T.....
Maldives	??????????
<i>H. planifrons</i>C.....G.....G.....C.....C.....C.....C.....C.....C.....C.....
	170	180	190	200	210	220	230	240
MZUF1956	ACAAACACAG	CGTCTCGATC	CGTCGCAT??	??????????	??????????	??????????	??????????	??????????
QM-J2106T.....
PEM292CAT	ATTTCGCGAG	ACGTTAATTA	TGGCTGAATT	ATCGGATACC	TACATGCAAA
PEM1960CAT	ATTT??????	??????????	??????????	??????????	??????????
MaldivesCAT	ATTTCGCGAG	ACGTTAATTA	TGGCTGAATT	ATCGGATACC	TACATGCAAA
<i>H. planifrons</i>T.....C.....	ATTTCGCGAG	ACGTCACACTA	CGGCTGAATT	ATCGGATACC	TACATGCAAA
	250	260	270	280	290	300	310	320
MZUF1956	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
QM-J2106	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
PEM292	CGGAGCGCTCT	ATAATCTTTA	TCTGCTCTTA	CGACACATC	GGACGCGGCT	TATATTATGG	TTCCTACATC	TTCCAGAGAA
PEM1960	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
Maldives	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
<i>H. planifrons</i>	CGGAGCGCTCT	ATAATCTTTA	TCTGCTCTTA	CGACATATC	GGACGCGGCT	TATACTACGG	CTCTTACATC	TTCCAGAGAA
	330	340						
MZUF1956	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
QM-J2106	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
PEM292	CATGAATAT	TGGGGTAGTC	CTACTCTTT
PEM1960	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
Maldives	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????
<i>H. planifrons</i>	CATGAATAT	CGGAGTAGTC	CTACTCTTC

Figure 2. Continued.

whale *M. hectori*, to 13.12% from Arnoux's beaked whale *B. arnuxii*). At the mtDNA cytochrome *b*, the Somali and Maldivian specimens shared the same haplotype, which differed from that of the holotype specimen by one non-synonymous substitution. The haplotype possessed by the two South African specimens differed from that of the holotype by two transition substitutions (third position synonymous, first position non-synonymous; Fig. 2b). Over the maximum sequence length available (268 bp; PEM292), *I. pacificus* differed from all other beaked whales by an average of 15.16% (range: 11.74% from Hubbs' beaked whale *M. carlhubbsi*, to 19.51% from the ginkgo-tooth beaked whale *M. ginkgodens*). Similar patterns of divergence (*i.e.*, relatively low within species and relatively high between species) have been observed for both loci among other ziphiid taxa, including intraspecific non-synonymous substitutions at the cytochrome *b* (Dalebout 2002, Dalebout *et al.* 1998).

Morphological Description

Here we present the first images of the external appearance and teeth of confirmed specimens of this species. The only previously published figures of known Longman's beaked whale are of the crania and mandibles of the holotype and Somali specimens (Longman 1926; Azzaroli 1968; Moore 1968, 1972). No teeth were found with either specimen. For clarity, Ross' (1984) description of the South African specimen, PEM292, is repeated here.

External appearance—Overall, the body form of juvenile Longman's beaked whales

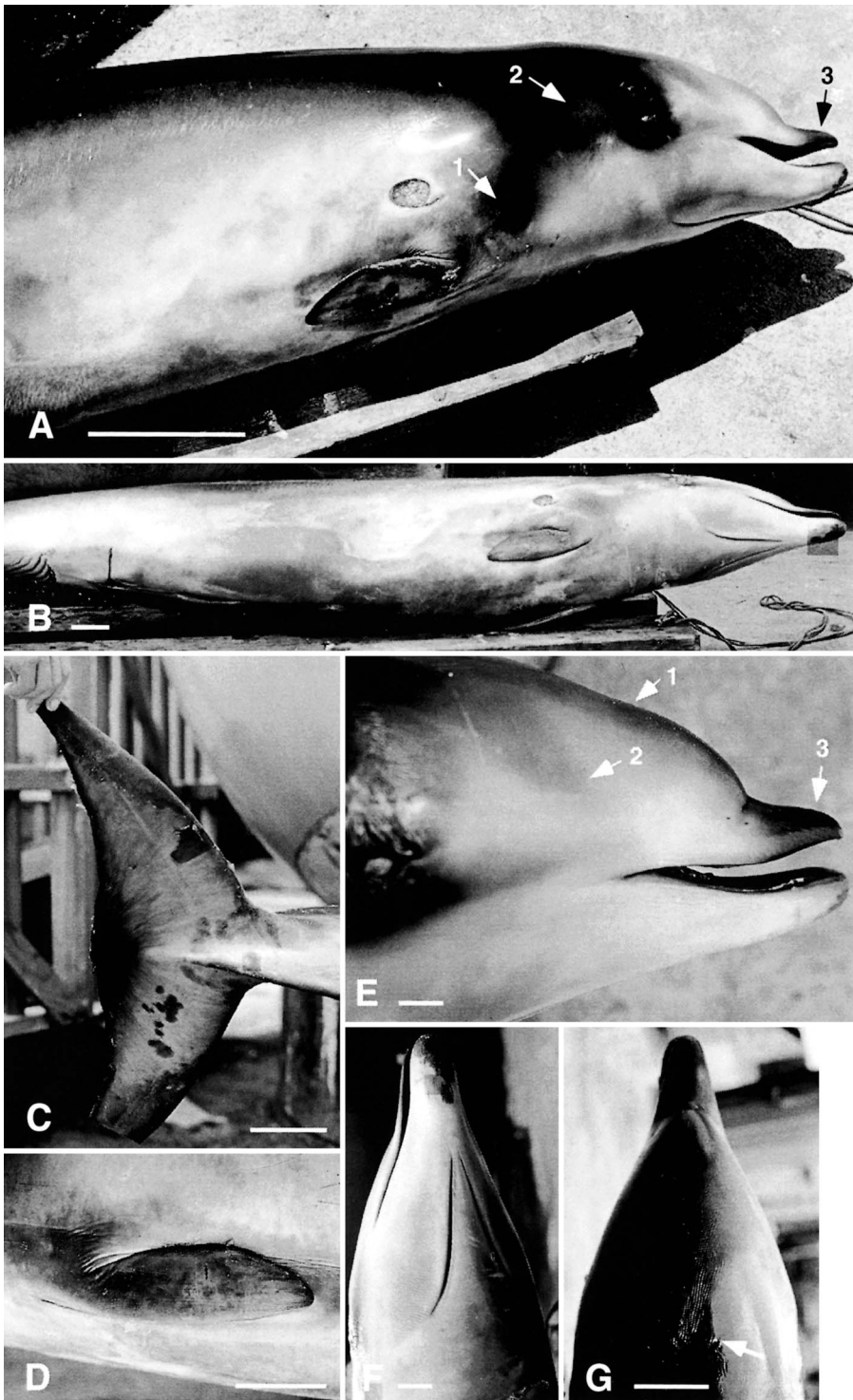
was similar to, though more slender than, juvenile *H. planifrons* of a similar size (Fig. 3, PEM292, 291 cm total length [TL]; PEM1960, 363 cm TL; for comparison see Fig. 4, *H. planifrons* AUNZ Hpl01, ~300 cm TL; AUNZ Hpl03, 368 cm TL). The small dorsal fin was set far back on the body and sloped rearwards on its anterior edge with a markedly falcate trailing edge. The melon was well rounded in profile and sloped evenly to meet the rostrum at $\sim 75^\circ$ (Fig. 3E, I). The beak was short and stout in juveniles of both *I. pacificus* and *H. planifrons*, but in the latter species the melon was more swollen and distinctly broader antero-dorsally (e.g., Fig. 4C).

In profile, the melon of the Maldivian adult female was similar in form and size to that of the South African juveniles. The melon rose above the level of the neck over the cranium and descended to meet the rostrum at $\sim 75^\circ$ (Fig. 5A, arrow 1). In contrast, the melon meets the rostrum at $\sim 90^\circ$ or more in *H. planifrons* (e.g., Fig. 4C, arrow). The rostrum was moderately long and slender. Taking into account distortion due to decomposition and associated swelling, the Maldivian female nonetheless appeared similar in overall robustness to *Hyperoodon* and *Ziphius* (Fig. 5B). In comparison, *Mesoplodon* spp. are generally laterally compressed and deep-bodied (e.g., see Mead 1989a, fig. 1). The melon was also larger and more pronounced than that of *Mesoplodon* spp. There was no evidence of tooth eruption in life (Fig. 5A, arrow 2) despite careful checking during the examination of the stranding. Other observed features common to all ziphiids include the lack of a notch in the tail fluke and small pectoral fins that tuck into well-defined depressions in the body wall (termed "flipper pockets" by Mead *et al.* 1982). These flipper pockets were visible in the calves (Fig. 3B, D, I) but not the adult female (Fig. 5), probably due to decomposition and bloating. The horns of the crescent-shaped blowhole pointed anteriorly (only those of *Berardius* spp. point posteriorly). External measurements are given in Table 2.

Color pattern—Much of the following description of neonate-juvenile color pattern is based on the South Africa specimen, PEM292, which was examined when fresh (Ross 1984; Fig. 3A–H). Posterior to the blowhole, the entire dorsal surface was black, becoming dark gray laterally prior to merging smoothly with the white of the ventral surface. Posterior to the eye, the black of the dorsum extended ventrally in a broad band towards the anterior insertion of the flipper, becoming gray as it did so (Fig. 3A, arrow 1). This feature appears to be absent in *H. planifrons* (e.g., Fig. 4A, arrow), but may occur in *Tasmacetus* (see Baker 1999, p. 87). A dark band of black extended ventrally from the blowhole to join a black patch surrounding the eye. A small lighter patch was embedded in the area of dark pigmentation posterior to the eye (Fig. 3A, arrow 2). Anterior to the blowhole, dark gray pigment extended along the mid-line as far as the apex of the melon (Fig. 3E; arrow 1), in an antero-lateral streak over the upper half of the melon and anterior to the eye (Fig. 3E; arrow 2). Much of the upper jaw and dorsal margin of the lower jaw tip were black (Fig. 3A, E;

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Figure 3. External appearance of juvenile Longman's beaked whales; PEM292: (A) lateral view of body, scale bar = 30 cm; (B) oblique ventral view, scale bar = 10 cm; (C) ventral view of flukes, scale bar = 10 cm; (D) left flipper, scale bar = 10 cm; (E) lateral view of head, scale bar = 5 cm; (F) oblique ventral view of head, scale bar = 5 cm; (G) dorsal view of head, scale bar = 10 cm (arrow indicates right anterior tip of blowhole); (H) dorsal fin, scale bar = 10 cm; PEM1960 (I) lateral view of body, scale bar = 50 cm; Photocredits: (A–H) G. J. B. Ross, (I) V. Peddemors. Arrows (except G), see text for discussion.



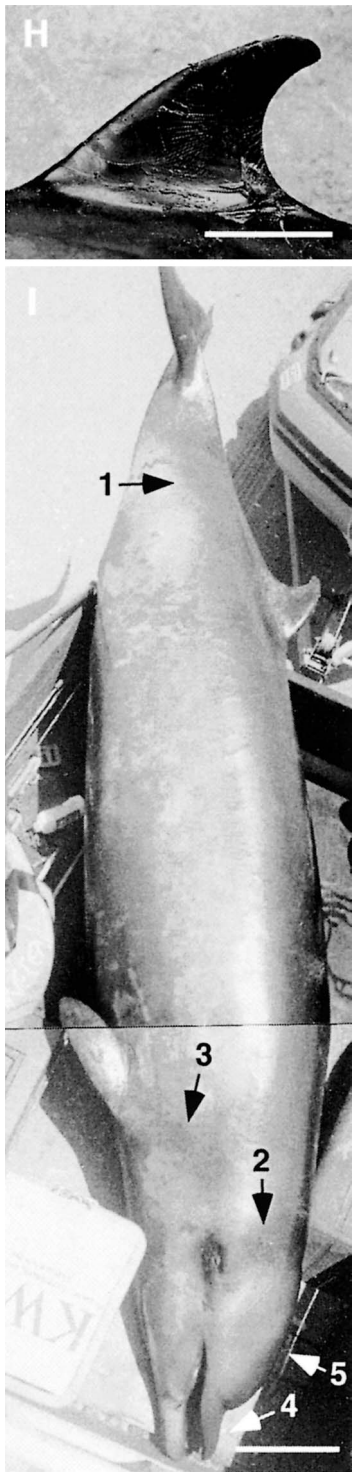


Figure 3. Continued.

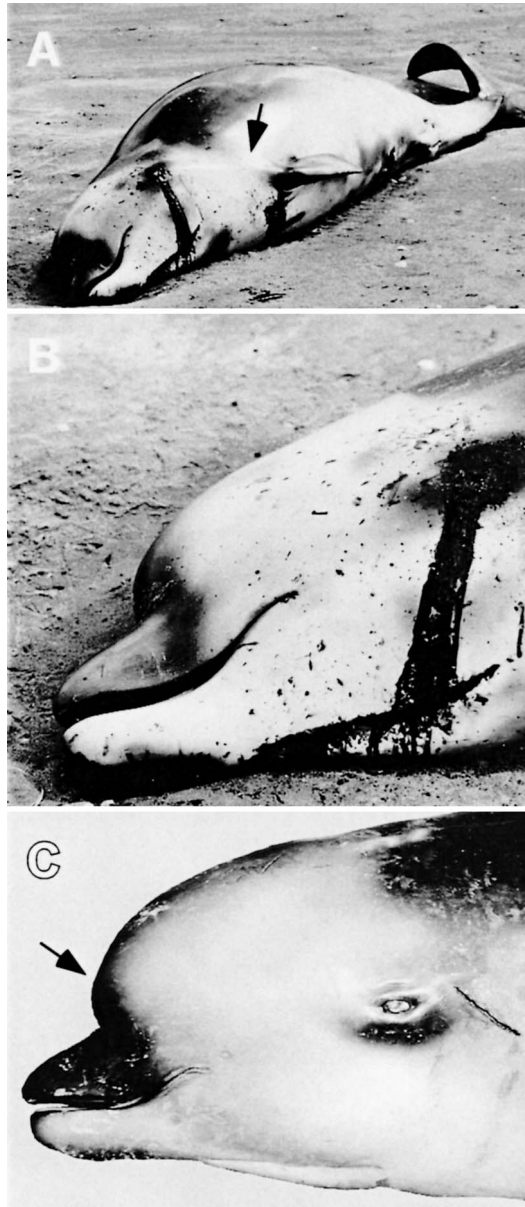


Figure 4. External appearance of juvenile southern bottlenose whales, *Hyperoodon planifrons*, from strandings in New Zealand; AUNZ Hpl03 (Ohope, Whakatane, 1 April 1996. Female; TL 368 cm): (A) antero-lateral view of body; (B) lateral view of head. AUNZ Hpl01 (Orere Pt., Firth of Thames, 7 December 1994. Female; TL ~300 cm): (C) lateral view of head. Arrows, see text for discussion. Photocredits: (A–B) R. Tully, (C) T. Jones.

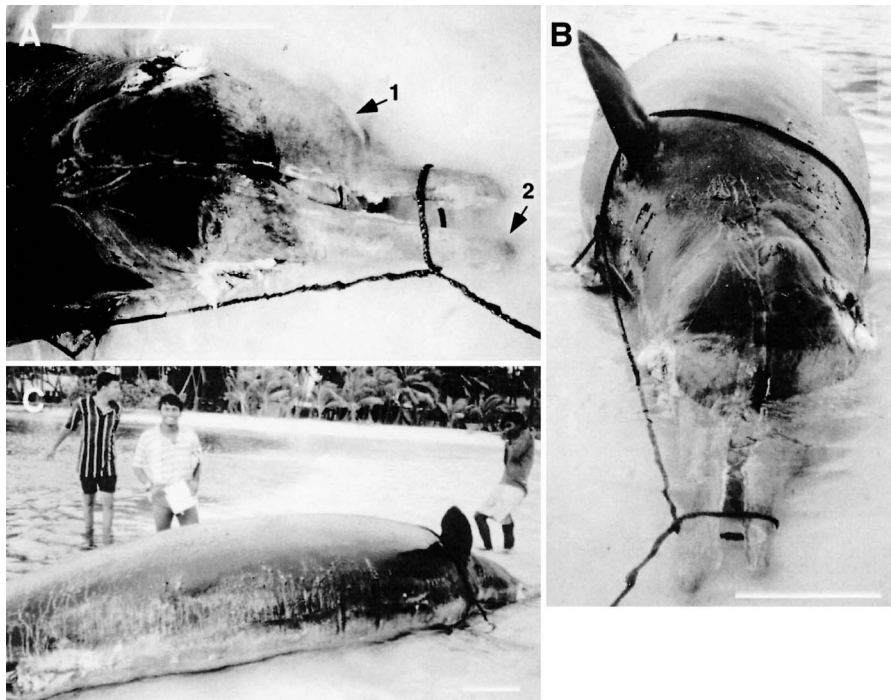


Figure 5. External appearance of adult female Longman's beaked whale; Republic of Maldives: (A) lateral view of head; (B) view of body from anterior perspective; (C) ventral view of anterior two-thirds of body. All scale bars = 50 cm. Arrows, see text for discussion. Photocredit: A. Hafiz.

arrow 3 both figures), in contrast to the white of the rest of the face, lower jaw, and throat. The outer surface of the flippers was black, while the inner surface was white (Fig. 3D). The posterior margin and the anterior third of the dorsal fin were dark gray to black and enclosed a white blaze (Fig. 3H). In the posterior half of the caudal peduncle, the dark gray of the dorsal margin extended to the mid-depth of the peduncle. Ventrally, the skin in this region was pigmented with fine flecks and streaks of dark and pale gray. The dorsal surface of the flukes was black. On the ventral surface, the margins of the flukes were black. In the middle third of the trailing edge of the flukes, the dark margin broadened anteriorly as far as the junction of the caudal peduncle and the fluke surface. From the anterior margin, numerous fine gray streaks radiated across the white background of the ventral surface as far as the leading edge of the flukes (Fig. 3C).

Much of the coloration of the second juvenile (PEM1960) was lost though exposure to the sun. However, elements of the color pattern described for PEM292 were discernible, including the extension of the dark dorsal pigmentation to mid-depth of the body and more posteriorly onto the ventral caudal peduncle (Fig. 3I, arrow 1), the dark strips linking the dorsal pigmentation with the eye patch and the flipper (Fig. 3I, arrows 2 and 3), the dark upper jaw, and white lower jaw (Fig. 3I, arrow 4). Overall, the light appearance of the head and melon was clearer in this animal than in PEM292 and

Table 2. External measurements for Longman's beaked whale. Where two numbers are given, the first is from the right hand side and the second from the left hand side. % TL, percentage of total length.

	South Africa PEM 292		South Africa PEM1960		Maldives —	
	cm	% TL	cm	% TL	cm	% TL
Sex/age class	male/neonate		male/juvenile		female/adult	
Total length	291.0	100	363.0	100	596.0 ^a	100
Beak tip to centre of blowhole	41.0	14	50.0	14	—	—
Beak tip to centre of eye	43.0	15	54.5	15	100.0 ^a	17
Beak tip to apex of melon	9.5	3	—	—	—	—
Beak tip to angle of mouth	26.0	9	34.0	9	—	—
Beak tip to anterior insertion of flipper	71.0	24	—	—	—	—
Beak tip to centre of umbilicus	145.0	50	175.0	48	—	—
Beak tip to genital slit (centre)	178.0	61	220.0	61	—	—
Beak tip to anus	203.0	70	258.0	71	—	—
Beak tip to tip of dorsal fin	202.0	69	249.0	69	—	—
Beak tip to anterior insertion of dorsal fin	182.0	63	224.0	62	385.0	65
Beak tip to post. end of throat creases	39.0	13	48.0	13	—	—
Length of genital slit	17.0	6	15.0	4	—	—
Length of mammary slits	3.5	1	—	—	—	—
Length of anal opening	8.0	3	10.0	3	—	—
Girth at axilla	132.0	45	—	—	—	—
Maximum girth	142.0	49	—	—	384.0 ^b	64
Girth at anus	106.0	36	—	—	—	—
Projection of lower jaw beyond rostrum tip	1.2	0	—	—	—	—
Length of eye opening	2.7	1	—	—	5.0	1
Centre of eye to angle of mouth	19.0	7	—	—	—	—
Centre of eye to centre of blowhole	27.0/ 23.0	8.6 ^c	—	—	—	—
Blowhole width	8.5	3	—	—	—	—
Length of throat grooves	25.0	9	29.0	8	—	—
Flipper length, anterior	29.0	10	26.0	7	55.0	9
Flipper length, posterior	17.5	6	22.0	6	—	—
Flipper width, maximum	8.0	3	9.0	2	—	—
Fluke width	62.0	21	78.0	21	—	—
Fluke depth	20.5	7	22.0	6	—	—
Depth of fluke notch	NA	—	NA	—	—	—
Dorsal fin height	13.0	4	18.0	5	—	—
Length dorsal fin base	21.0	7	24.0	7	—	—
Weight	228 kg	—	510 kg	—	—	—

^a Curvilinear length.

^b Decomposition may have caused some bloating.

^c Taken from mean of left and right hand measurements.

highlighted the same features, particularly the patch of gray pigment extending antero-laterally across the upper part of the melon (Fig. 3I, arrow 5).

Much of the coloration of the Maldivian female was also lost through exposure to the sun. However, dark flecks and streaks were apparent on the pale ventral surface (Fig. 5C). Note that the detail in color pattern provided from the calves may not represent that of adults, as color patterns are known to change with age for some ziphiids (e.g., Mead 1989a, b).

Cranial osteology—Moore (1968) proposed the new genus *Indopacetus* for Longman's beaked whale based on four distinctive cranial features observed in the two skulls described from Queensland and Somalia (Longman 1926, Azzaroli 1968): (1) the frontal bones occupy an area of the vertex of the skull approximating or exceeding that occupied by the nasal bones; (2) there is minimal extension of the premaxillary crest on the vertex between the nasal and maxillary bones, or between the frontal and maxillary bones; (3) a deep groove about half the length of the orbit is present on the dorso-lateral margin of the maxillary bone above the orbit; and (4) as seen in dorsal view, the premaxillae retain an even width to about the midlength of the rostrum, where they may expand slightly before converging again towards the tip of the rostrum. This expansion differs from the changes that occur in the rostrum of adult male *M. densirostris* (e.g., Mead 1989a, fig. 15D), in which the maxillae narrow on each side for several centimeters anterior to the base of the rostrum, presenting a "pinched" appearance, before broadening again to its original breadth near the mid-length.

All four of these features were observed on the Kenyan skull (Fig. 6A–C, arrows) and confirm that this specimen represents Longman's beaked whale. Despite its youth, the skull of the juvenile, PEM1960, also displayed these features (Fig. 7). Features 1 and 2, relating to the comparative size and arrangement of bones on the vertex, were particularly clear (Fig. 7D), as was feature 3, the maxillary groove (Fig. 7C, arrow). At the time of writing, the Maldivian skull (Fig. 6D–F) was not sufficiently clean to examine suture details on the vertex. However, the anterior half of the rostrum narrowed slightly near the mid-length then widens again (Fig. 6D), similar to that observed in the other *Indopacetus* skulls.

The width of the rostrum at mid-length was due largely to the maxillary bones which form a broad, elongate flange along each side of the rostrum. In the holotype (Queensland), Somali, and Kenyan skulls, these bones formed an even concave curve from the cranium to the tip of the rostrum, as seen in lateral views (Fig. 6C, E; Fig. 7C). This arrangement may serve to strengthen the rostrum. The rostrum of *Tasmacetus* is very similar, both in its width for the proximal half of the rostrum and the curvature of the maxillary bones. However, in contrast to its width, the depth of the rostrum at mid-length was proportionately less in *Indopacetus* than in other ziphiids, as reflected by the ratio of rostrum width/depth at mid-length (Fig. 8).

The distinctive vertex of the *Indopacetus* skull is formed of the postero-dorsal portions of the left and right nasal and frontal bones, sandwiched between the dorsal rim of the supraoccipital bone posteriorly, the maxillary bones laterally, the left and right nasal bones anteriorly, and the premaxillary crests antero-laterally (e.g., Fig. 7D). The nasal and frontal bones are irregular in shape. The nasals protrude anteriorly between the maxillary crests, extending farthest along the suture line that separates them. However, they do not protrude anteriorly beyond the line connecting the anterior faces of the maxillary crests (Fig. 6A, D; 7D).

The form of the vertex in *Indopacetus* contrasts with that of other ziphiid genera (Fig. 9): in *Berardius* and *Tasmacetus*, the nasal bones occupy an area on the vertex far

exceeding that of the frontals and premaxillae; in *Ziphius*, the nasals are also enlarged and protrude anteriorly to overhang the external bony nares; in *Mesoplodon*, the cranial vertex is extremely well developed (Mead 1989a) with prominent premaxillary crests; and, in *Hyperoodon*, the cranial vertex is developed to a similar extent as that in *Mesoplodon* spp. (Moore 1968). *Hyperoodon* spp. are further distinguished from other genera by the prominent development of their maxillary crests (e.g., Mead 1989b, fig. 2). While a detailed comparison of vertex structure among ziphiids (including the potential use of these features to infer evolutionary relationships) is outside the scope of this paper, the distinctiveness of *Indopacetus* from *Mesoplodon* spp. (and also *Hyperoodon* spp.) is nonetheless apparent (Fig. 9).

The nasal and frontal bones on the vertex show different degrees of fusion in the three *Indopacetus* skulls in which suture details can be observed, presumably as a reflection of age. Those of the South African (PEM1960) specimen were not fused and easily distinguishable, those in the holotype were far less discernible, and those of the Kenyan skull were almost obliterated. There was very little difference, other than size, in the shape and relative placement of the nasals and frontal bones in the skulls of the adults and juvenile (Fig. 6, 7).

Comparison of cranial measurements (Table 3) suggested that the Kenyan and Somali skulls were very similar in overall structure to the holotype.³ However the Maldivian skull was consistently and distinctly narrower than those of the other three adults in a range of measurements: breadth of the cranium (Table 3, measurements 17–20); width of the premaxillae along their entire length and the width of the rostrum at mid-length (Table 3, measurements 29, 32–35). The least distance between the premaxillary foramina was also smaller in this specimen. It is possible that these differences reflect sexual dimorphism, as has been observed in other ziphiid species (e.g., Heyning 1989; Mead 1989a, b). Alternatively, this may be due to slight differences in techniques of skull measurement by different researchers.

Other features of the skull described previously for the holotype and Somali skulls (Moore 1972) were also apparent in the Kenyan skull and that of the juvenile, PEM1960. The lacrimal bone was large and hood-shaped, and was the primary contributor to the antorbital tubercle (e.g., Fig. 6C). This feature also differentiates *Indopacetus* from *Mesoplodon* spp. (Mead 1989a). In PEM1960, the Kenyan and Maldivian skulls, mesorostral ossification was minimal. In the latter specimen (adult female) the mesorostral ossification rose above the rim of the mesorostral canal immediately anterior to the nares but was restricted to the posterior portion of the mesorostral canal. A similar situation was observed in the holotype and Somali specimens. In adult males of *Mesoplodon* spp. the mesorostral canal is usually filled in through proliferation of the vomer (Mead 1989a).

Teeth and dentition—Three of the specimens described in this paper provide the first opportunity to examine the teeth of *Indopacetus*. The dentition comprised a single pair of teeth which are set close to the tip of the jaw (Fig. 7E, 10). The teeth were very similar in shape to that predicted by Mead (1989a).

The teeth of the neonate, PEM292, were fully enclosed in the terminal alveoli (tooth sockets). They lay 3–4 mm from the tip of the mandible and were angled

³ Other than several longitudinal measurements of the Somalian skull which include the rostrum and appear inconsistent in proportion, reflecting the difficulty of estimating corrections for damage.

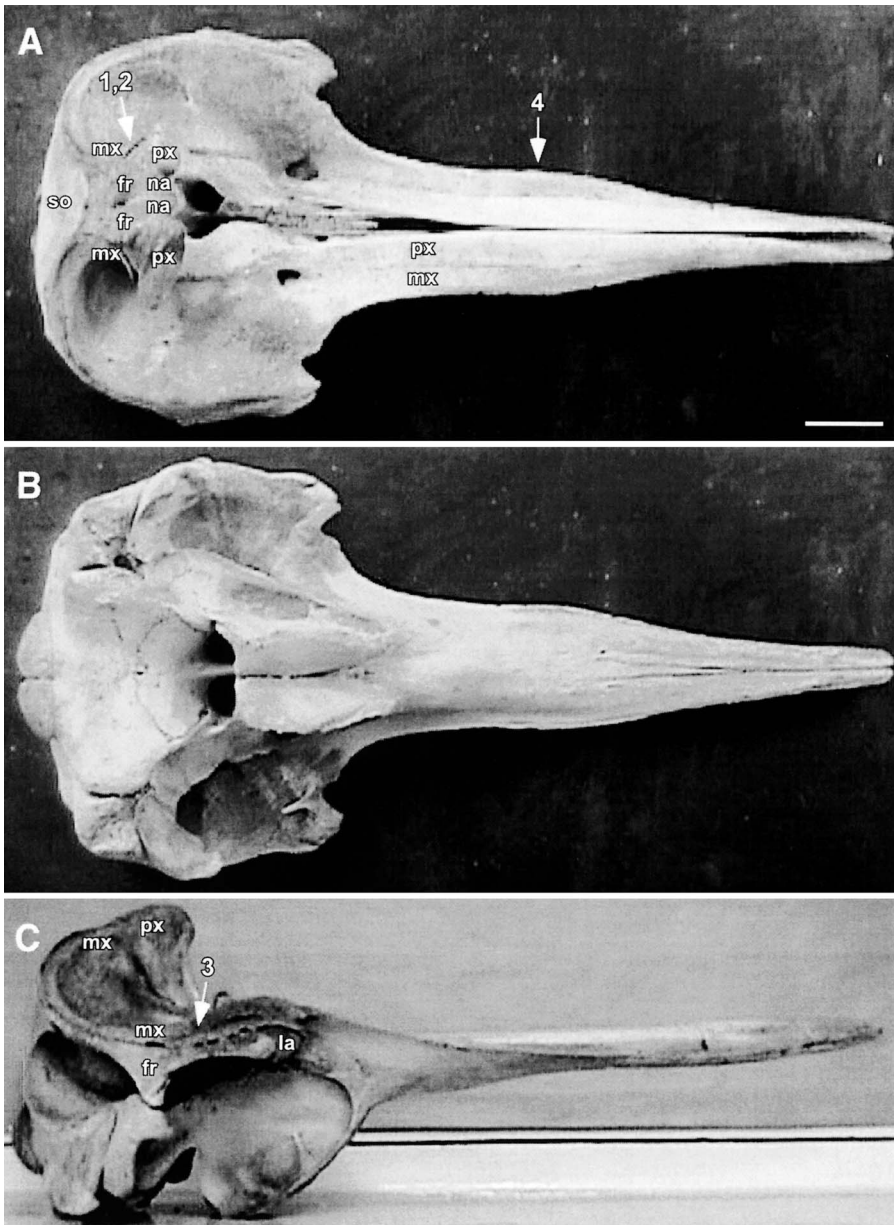


Figure 6. Skulls of mature Longman's beaked whales; OM7622, Kenya: (A) dorsal view; (B) ventral view; (C) lateral view (scale bar = 10 cm, images A–C). Republic of Maldives: (D) dorsal view; (E) ventral view; (F) lateral view (scale bar = 30 cm, images D–F). Arrows (numbered as in text) highlight diagnostic cranial features discussed by Moore (1968). fr, frontal; la, lacrimal; na, nasal; mx, maxilla; px, premaxilla; so, supraoccipital. Photocredits: (A–C) H. L. Hinsz, (D–H) R. C. Anderson.

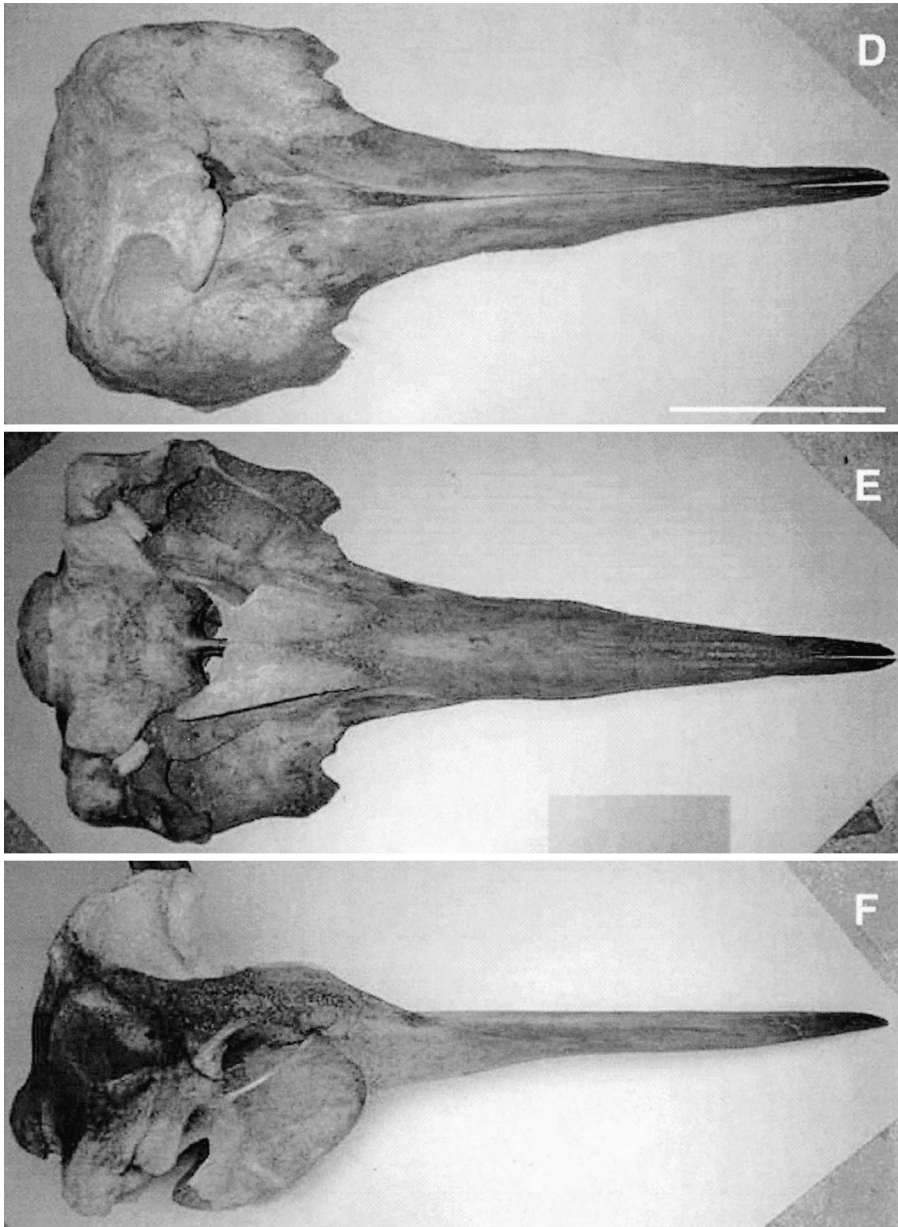


Figure 6. Continued.

forward at about 45° (Fig. 10E, X-ray of beak). In lateral view each tooth appeared as a hollow, evenly tapered cone, 20 mm in length and 11.5 mm in diameter at the base. The prenatal dentine was ~ 1 mm at its thickest part, near the apex of the pulp cavity. The teeth of the juvenile, PEM1960 (Fig. 7E) were similar in form;

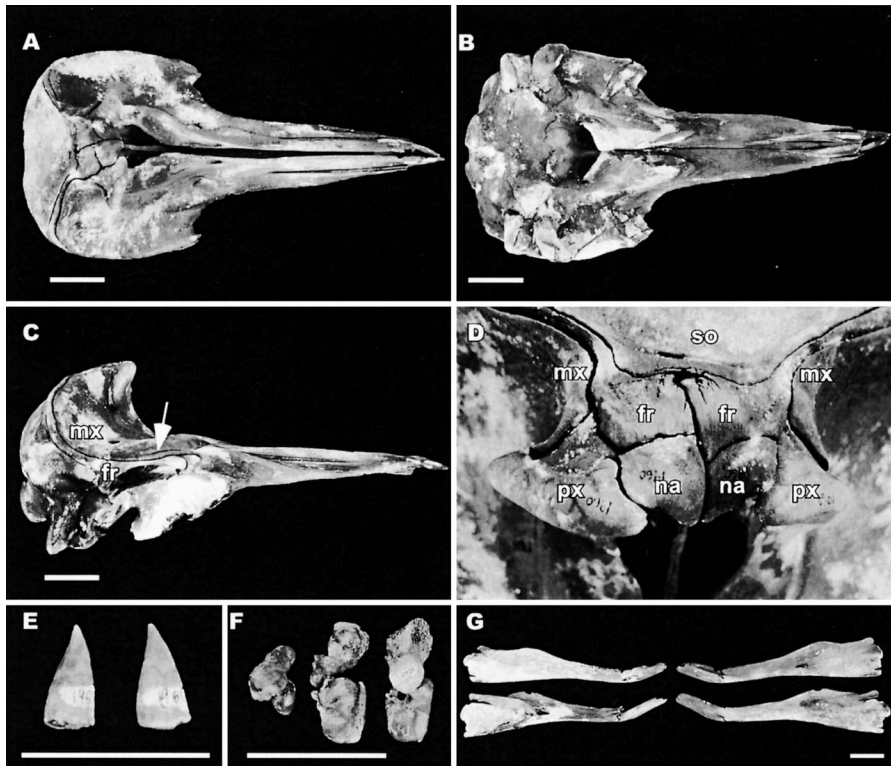


Figure 7. Skull, teeth and earbones of juvenile Longman's beaked whale; PEM1960: (A) dorsal view of skull; (B) ventral view of skull; (C) lateral view of skull; (D) close-up of cranial vertex; (E) lateral view of teeth; (F) periotic and tympanic bones; (G) lateral view of exterior and interior of mandibular rami. Arrow highlights the position of the maxillary groove (Moore 1968). fr, frontal; na, nasal; mx, maxilla; px, premaxilla; so, supraoccipital. Scale bars for all images except E = 10 cm. Scale bar for image E = 5 cm. Photocredit: P. B. Best.

slightly longer (27 mm) but a similar width at the base ($\sim 11 \text{ mm} \times 13 \text{ mm}$). Mandibular measurements are provided in Table 4.

The teeth of the adult female were also roughly conical in shape (Fig. 10B). *In situ* a small portion of the teeth protruded from the alveoli (Fig. 10A; note that the teeth have likely fallen slightly forwards out of the alveoli as the jaw was raised up to vertical for this photograph). However, in life this emergent portion was apparently covered by thick gum tissue such that the teeth were not visible (Fig. 5A, arrow 2), nor could they be detected through gentle palpation post mortem. Among all beaked whales (except *Berardius* spp.), only mature males have erupted teeth. (In *Tasmacetus*, both sexes have a full complement of teeth, but the larger apical pair erupt only in adult males; Mead 1989c). From these observations we assume that *Indopacetus* follows the same pattern.

The teeth of the adult female were oval in cross-section at the base due to slight lateral (transverse) flattening (Fig. 10C). A thick cementum sheath covered the entire base of both teeth to a thickness of $\sim 2\text{--}4 \text{ mm}$ (Fig. 10B). There was no evidence that this sheath was pathological, and it is likely that this is the normal

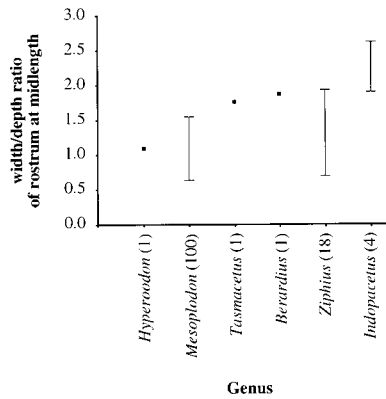


Figure 8. Width/depth ratio of rostrum at mid-length for all ziphiid genera. Number of specimens examined for each genus shown in brackets. Figures derived from the specimens described in this paper, unpublished data from G. J. B. Ross, and the following sources: Azzaroli (1968), Dixon (1970), Kasuya and Nishiwaki (1971), McCann (1962*a, b*), McCann and Talbot (1963), Miyasaki *et al.* (1987), Moore (1963), Nishiwaki and Kamiya (1958), Oliver (1937), Omura (1972), Reyes *et al.* (1991), Ross (1984), Ross and Teitz (1972), Scott and Lord (1920), and Zerbini and Secchi (2001).

condition for the species. A similar cementum sheath has been observed on the teeth of many female *Mesoplodon* beaked whales and some female *Ziphius*.⁴ Most *Mesoplodon* spp. have teeth composed of tightly packed layers of dentine covered in a thin external layer of cementum which extends up from the root. Only in adult males with hypertrophied teeth does tooth growth continue through substantial deposition of cementum (Perrin and Myrick 1980). The left tooth of the Maldivian female bore a circular cavity, ~6 mm in diameter and 4–5 mm deep, on its medial surface through which the internal osteodentine was visible. This cavity is thought to be a resorption lesion resulting from a tooth abscess. This would fit with the clinical description of the tooth crown being covered by soft tissue.⁵ There was no visible wear on the teeth. A large part of the pulp cavity of the tooth of the adult female was still open (Fig. 10C, D), forming a hollow conical space, ~10 mm in diameter and ~13 mm in depth. A number of nodules were visible on the walls of the pulp cavity, and are thought to be pulp stones or secondary centers of dentine deposition. Assuming the size of the teeth in PEM292 is typical for neonate *Indopacetus*, the tooth of the adult female has almost doubled in length since birth.

Beaked whales of the genera *Hyperoodon*, *Tasmacetus*, and *Ziphius* have comparatively simple conelike teeth set at the apex of the lower jaw (*e.g.*, Moore 1968), similar to those now observed in at least adult female *Indopacetus*. Apical, conelike teeth are likely to represent the ancestral form among ziphiids (Moore 1968). In *Mesoplodon* beaked whales the teeth are generally derived and specialized (*e.g.*, Mead 1989*a*). Only three species of *Mesoplodon* have apical teeth (*M. hectori*, *M.*

⁴ Personal communication from J. G. Mead, Smithsonian National Museum of Natural History, Washington, DC, e-mail, 4 October 2001.

⁵ Personal communication from F. Verstraete, Department of Radiological and Surgical Sciences, School of Veterinary Medicine, University of California, Davis, CA, e-mail, 12 June 2001.

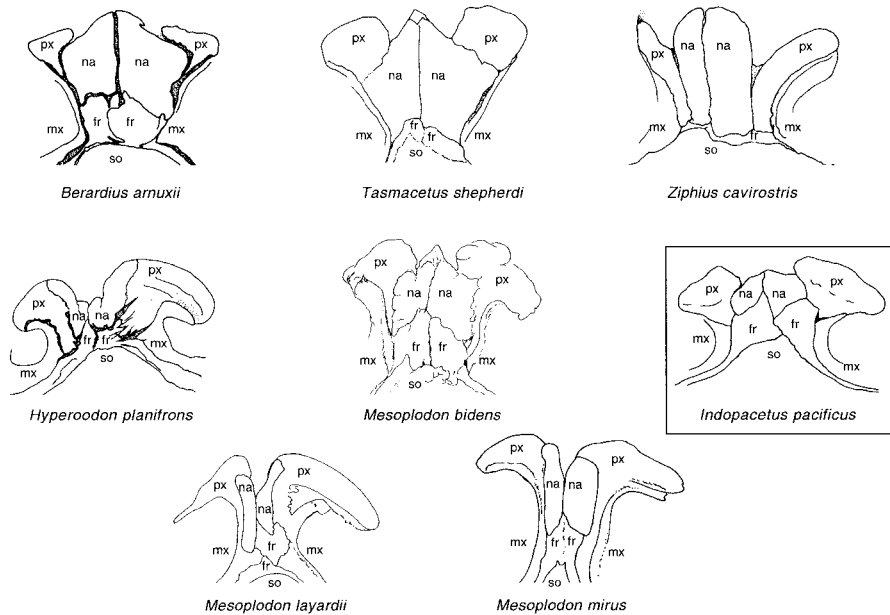


Figure 9. The form in the dorsal surface of the vertex varies considerably within and between the six extant ziphiid genera. The three *Mesoplodon* spp. shown reflect the range of morphology in this genus: the type species of the genus, *M. bidens* (USNM504146, Mead 1989a); *M. layardii* (RNP 326, Goodall 1978); and *M. mirus* (SAM 33295, McCann and Talbot 1963). Information and sources for the other genera are: *Berardius arnuxii* (DM 183, Moore 1968); *Hyperoodon planifrons* (FMNH 15553, Moore 1968); *Tasmacetus shepherdi* (UCM 1063, Moore 1968); *Indopacetus pacificus* (M4854, Azzaroli 1968) and *Ziphius cavirostris* (FMNH 99362, Moore 1968). fr, frontal; mx, maxillary; na, nasal; px, premaxillary; so, supraoccipital.

mirus, and *M. perrini*). In other *Mesoplodon* spp. the single pair of teeth is set back from the apex of the jaw. *Mesoplodon* teeth are also laterally flattened, a feature thought to distinguish this genus from all others except *Berardius* (Moore 1968). However, the teeth of the recently described species, *M. peruvianus*, are more oval in cross-section (Reyes *et al.* 1991) and, together with those of *M. mirus*, are similar in form to those of *Ziphius*. So while tooth form in most *Mesoplodon* spp. is derived, some have still retained simple conelike teeth.

The alveoli of *Indopacetus* are shallow compared to those of *Mesoplodon* spp., especially males. Moore interpreted the holotype as representing an "old adult male [in which the alveoli] become progressively at least as shallow as 30 mm" (Moore 1968, p. 282). In contrast, the alveoli of aging *Mesoplodon* males remain deep, often containing more than half the length of the tooth, and probably exceed 30 mm in depth (Moore 1968). The alveoli of the holotype and Maldivian adult female were very similar in length and width (Table 4, measurements 9 and 10), suggesting that the teeth they supported were also similar in form and size. Moore's (1968) suggestion that alveolus depth is diagnostic for this species should therefore be re-evaluated to include both sexes. Alternatively, it is possible that the holotype does not represent an adult male.

Postcranial osteology—The vertebral count of PEM292 was C7 T10 L12 Cd7+ = 36+. Most of the caudal vertebrae remaining in the frozen tailstock of this specimen were lost in storage prior to preparation. The first five cervical vertebrae were fused. The anterior seven pairs of ribs were double-headed. The tubercle of the seventh rib articulated with the superior transverse process. On the eighth thoracic vertebra, there was an abrupt replacement of the superior transverse process by an inferior transverse process. Very little skeletal material was retrieved from PEM1960. However, there were ten intact ribs on one side, of which the first seven were double-headed. The vertebral count of the Maldivian adult female was C7 T10 L9 Cd15+ = 41+. A small number of caudal vertebrae were lost in preparation. The anterior seven pairs of ribs were double-headed and the last three had a single articulation. The first five cervical vertebrae were fused, although the fifth vertebra was only partly attached. The sixth and seventh cervicals were quite separate. Each epiphysis was fused to its respective vertebral body. The larger number of lumbar vertebrae in PEM292 probably reflects the young age of this specimen and the consequent difficulty in detecting the position of the first chevron bone. Based on examination of these specimens, *I. pacificus* appears to have ten pairs of ribs, although it is recognized that sample size is very small. No information is available regarding phalangeal formula.

Natural History

Ontogeny and reproduction—The testes of the smallest animal (PEM292; 291 cm TL) measured 41 × 14 mm and 40 × 15 mm and weighed 3.7 g and 3.2 g, respectively. Histological sections through the center of the testis showed abundant interstitial tissue and narrow tubules with a reduced or no lumen. The mean tubule diameter at the center and periphery of the testis at mid-length was 35 μ (Ross 1984).

In PEM292 the margins of the tongue were fimbriated, especially on the lateral edges, presumed to be related to suckling. The umbilicus appeared to be completely healed. However, on the right hand side of the body, at least six narrow, vertical, dark fetal folds were visible. Based on information from bottlenose dolphins *Tursiops* sp., where such fetal folds remain visible for up to a month after birth, it is likely that this animal was not more than a few weeks old (Ross 1984). As PEM292 stranded in early November, it was probably born in late September or October. The second juvenile, PEM1960, stranded in early August. Assuming that the length of PEM292 was close to the birth length in this species, PEM1960 (363 cm TL) may have been born during the previous season, and as such would be approximately eight to ten months old. No fetal folds were visible on this specimen. The Maldivian adult female, which stranded in mid-January, carried a fetus, which was 104 cm in length. No other measurements were taken of the fetus due to extensive decomposition.

Scarring and bite marks—A fresh cookie-cutter shark bite (*Isistius* sp.; Jones 1971) was present on the right side of the calf, PEM292, just above the flipper (Fig. 3A, B). A set of tooth rakes, probably caused by a large shark, was present on the ventral-left lateral surface of the body, near the caudal peduncle (Fig. 3B). There were no obvious scars on PEM1960. Fresh bites were noted on the flukes and dorsal fin of the Maldivian specimen, probably caused by large sharks while the animal was dead and drifting with the currents. Linear tooth rake scars potentially inflicted by conspecifics (e.g., Heyning 1984) were not observed on any of the animals examined.

Table 3. Cranial measurements for Longman's beaked whale. Measurements were made by the authors indicated in the table, following Moore (1972). E, estimate (e.g., due to uncertainty because of wear or breakage). No cranium is held for the South African specimen, PEM292. % CBL, percentage of condylobasal length.

Measurement	Queensland QM-J2106		Kenya OM7622		Maldives —		Somalia MZUF 1956		South Africa PEM1960 ^c	
	(Ross, <i>this paper</i>)		(Hinsz, <i>this paper</i>)		(Anderson, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)	
	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL
1. Condylobasal length	1,194	100	1,116 ^a	100	1,230	100	1,130 ^b	100	704	100
2. Length of rostrum; tip of beak to line connecting apices of antorbital notches	815	68	752	67	855	70	775	69	435	61.8
3. Tip of rostrum to posterior margin of pterygoid near mid-line	969	81	888	80	985	80	775	69	507	71.9
4. Tip of rostrum to most posterior extension of wing of pterygoid	1,011	85	912	82	1,045	85	—	—	540E	76.7
5. Tip of rostrum to most anterior extension of pterygoid	703	59	648	58	765	62	—	—	345	49.0
6. Tip of rostrum to most posterior extension of maxillaries between pterygoids on the palate	807	68	786	70	870	71	—	—	423	60.1
7. Tip of rostrum to most posterior extension of maxillary plate	1,117	93	1,056	95	1,160	94	1,110	98	649	92.2

Table 3. Continued.

Measurement	Queensland QM-J2106		Kenya OM7622		Maldives –		Somalia MZUF 1956		South Africa PEM1960 ^c	
	(Ross, <i>this paper</i>)		(Hinsz, <i>this paper</i>)		(Anderson, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)	
	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL
8. Tip of rostrum to anterior margin of superior nares	921	77	851	76	955	78	890	79	408	58.0
9. Tip of rostrum to most anterior point on premaxillary crest	979	82	894	80	995	81	940	83	522	74.1
10. Tip of rostrum to most posterior extension of temporal fossa	1,152	96	1,089	98	1,175	96	1,125	100	678	96.3
11. Tip of rostrum to most posterior extension of lateral tip of premaxillary crest	1,010	85	950	85	1,227	100	–	–	570	81.0
12. Tip of rostrum to most anterior extension of pterygoid sinus	749	63	679	61	–	–	–	–	373	53.0
13. Length of temporal fossa	180	15	186	17	160	13	155	14	118	16.7
14. Length of orbit	120	10	127	11	140	11	135	12	102	14.5
15. Length of right nasal on vertex of skull	49	4	88	8	–	–	86	8	38	5.4
16. Length of nasal suture	68	–	72	6	–	–	65	6	29	4.1

Table 3. Continued.

Measurement	Queensland QM-J2106		Kenya OM7622		Maldives —		Somalia MZUF 1956		South Africa PEM1960 ^c	
	(Ross, <i>this paper</i>)		(Hinsz, <i>this paper</i>)		(Anderson, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)	
	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL
17. Breadth of skull across postorbital process of frontals	528	44	538	48	505	41	480	42	337	47.9
18. Breadth of skull across zygomatic processes of squamosals	524	44	506	45	490	40	475	42	314	44.6
19. Breadth of skull across centers of orbits	504	42	502	45	460	37	470	42	322	45.7
20. Least breadth of skull across posterior margins of temporal fossae	317	27	323	29	320	26	315	28	257	36.4
21. Greatest span of occipital condyles	161	13	165	15	155	13	154	14	126	17.9
22. Greatest width of an occipital condyle	67	6	50	4	69	6	75	7	50	7.1
23. Greatest length of an occipital condyle	100	8	92	8	108	9	99	9	76	10.8
24. Greatest breadth of foramen magnum	54	5	54	5	52	4	54	5	57	8.1
25. Breadth of skull across exoccipitals	458	38	404	36	435	35	425	38	297	42.1

Table 3. Continued.

Measurement	Queensland QM-J2106		Kenya OM7622		Maldives –		Somalia MZUF 1956		South Africa PEM1960 ^c	
	(Ross, <i>this paper</i>)		(Hinsz, <i>this paper</i>)		(Anderson, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)	
	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL
26. Breadth of nasals on vertex	93	8	97	9	46E	–	85	8	72	10.2
27. Least distance between premaxillary crests	56	–	60	5	116E	–	–	–	113	16.0
28. Greatest extension of right premaxillary posterior of right nasal on vertex of skull	10	–	3	0	–	–	–	–	9	1.3
29. Greatest span of premaxillary crests	240	20	236	21	225	18	227	20	172	24.4
30. Least width (strictly transverse) of premaxillae where they narrow opposite superior nares	163	14	161	14	160	13	–	–	–	–
31. Greatest width of premaxillae anterior to place of previous measurement	168	14	162	15	–	–	–	–	–	–
32. Width of premaxillae at midlength of rostrum	89	7	89	8	73	6	76	7	52	7.4

Table 3. Continued.

Measurement	Queensland QM-J2106		Kenya OM7622		Maldives —		Somalia MZUF 1956		South Africa PEM1960 ^c	
	(Ross, <i>this paper</i>)		(Hinsz, <i>this paper</i>)		(Anderson, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)	
	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL
33. Width of rostrum in apices of antorbital notches	344	29	358	32	330	27	330	29	228	32.3
34. Width of rostrum in apices of premaxillary notches	—	—	297	27	280	23	302	27	184E	26.1
35. Greatest width of rostrum at mid-length of rostrum	125	10	144	13	116	9	128	11	99	14.0
36. Greatest depth of rostrum at mid-length of rostrum	55	5	55	5	61	5	58	5	48	6.8
37. Greatest transverse width of superior nares	90	8	81	7	82	7	89	8	72	10.2
38. Greatest inside width of inferior nares; at apices of pterygoid notches, on the pterygoids	—	—	—	—	128	10	125	11	96	13.6
39. Height of skull; distance between vertex of skull and most ventral point of pterygoids	433	36	425	38	450	37	420	37	276	39.2

Table 3. Continued.

Measurement	Queensland QM-J2106		Kenya OM7622		Maldives —		Somalia MZUF 1956		South Africa PEM1960 ^c	
	(Ross, <i>this paper</i>)		(Hinsz, <i>this paper</i>)		(Anderson, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)	
	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL	mm	% CBL
40. Greatest width of temporal fossa approximately at right angles to greatest length	115	10	111	10	—	—	112	10	65	9.2
41. Least distance between (main or anterior) maxillary foramina	119	10	119	11	120	10	118	10	78	11.0
42. Least distance between premaxillary foramina	43	4	36	3	25	2	37	3	23	3.3
43. Distance; posterior margin of left maxillary foramen to anterior extension of left maxillary prominence	93	—	105	9	—	—	87	8	44E	6.3
44. Greatest length of vomer visible at surface of palate	347	29	289	26	—	—	—	—	142	20.1

^a No adjustment made for the 25–50 mm broken off the tip of the rostrum.^b Broken fragment of rostrum included in measurements (Azzaroli 1968).^c Tip of rostrum broken but restored.

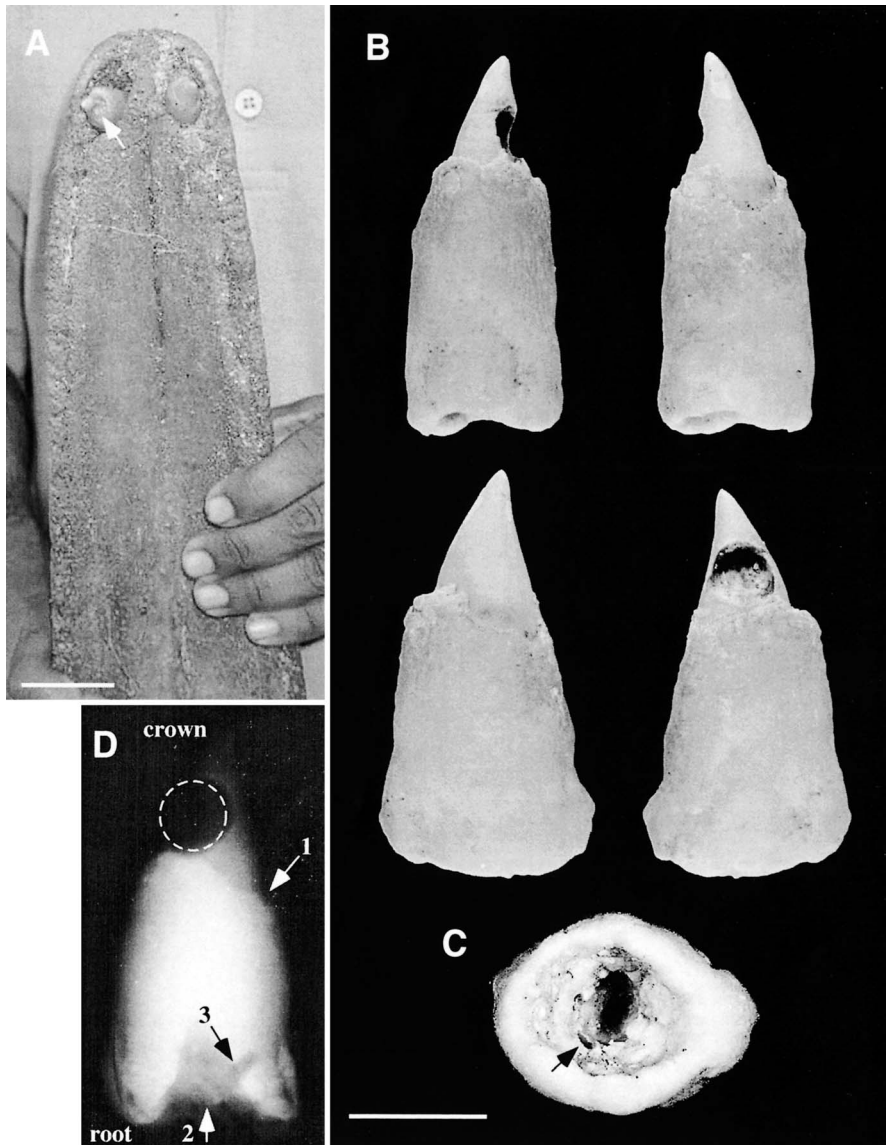


Figure 10. Teeth of Longman's beaked whales; adult female, Republic of Maldives: (A) dorsal view of mandible with teeth *in situ* arrow indicates position of cavity in left tooth (scale bar = 5 cm); (B) anterior, posterior, distal, and medial view of left tooth; (C) looking up into pulp cavity of left tooth arrow indicates position of drill hole resulting from DNA extraction procedure; (D) X-ray of left tooth. Arrow 1, cementum sheath; arrow 2, angle from which photo in C was taken; arrow 3, position of drill hole; dashed circle, position of cavity. Scale bar (images B–D) = 1 cm. (E) X-ray of beak of neonate, PEM292, in lateral view (scale bar = 2 cm). Photocredits: (A), R. C. Anderson; (B) and (C), I. MacDonald.

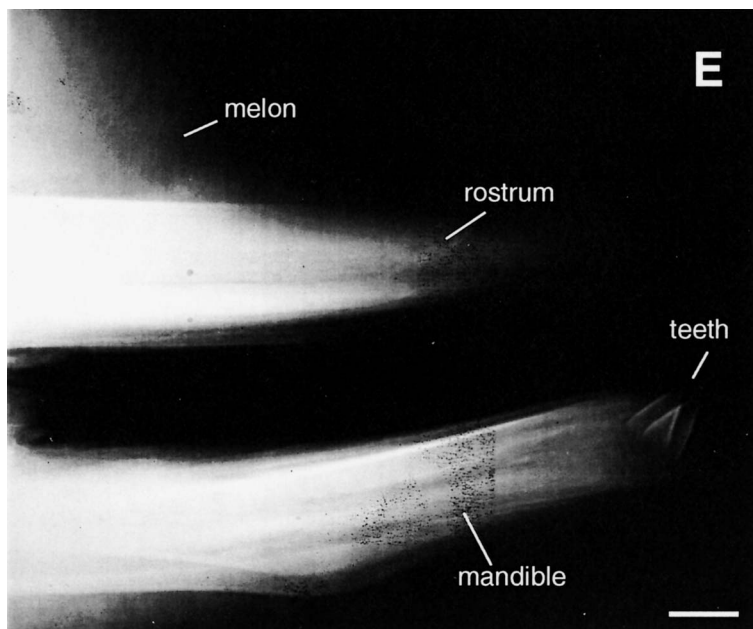


Figure 10. Continued.

Pollutant loads—Cockcroft *et al.* (1991) presented information on organochlorine pesticide loads for the South Africa neonate, PEM292. The blubber of this animal contained 1.2 ppm DDE, 0.4 ppm TDE, 2.99 ppm DDT, 0.07 ppm Dieldrin, and t-DDT' 1.6 ppm, with a DDE/t-DDT' ratio of 0.75. There were no detectable levels of PCBs. Given the young age of this animal, these pollutants would have been received through its mother's milk.

DISCUSSION

Longman's beaked whale is now known from a total of six specimens, from the western reaches of the tropical Pacific Ocean (21°10'S, 149°10'E), and the western, northern, and southern latitudes of the tropical Indian Ocean (range, 3°26'N, 73°26'E to 29°39'S, 31°36'E). The discovery of the South African animals has extended the known distribution in the Indian Ocean by more than 30° of latitude and suggests that this species may be parapatric with *H. planifrons* in the southern part of its range (Mead 1989b). Sightings in the tropical Indian and Pacific Oceans that have been attributed to *I. pacificus* (*i.e.*, animals identified as "tropical bottlenose whales" or "bottlenose-like" in appearance [*Hyperoodon* sp. or *H. planifrons*]) are listed in table 1 of Pitman *et al.* (1999). These sightings are distributed throughout tropical Indo-Pacific waters from Mörzer Bruyns' (1971) observations in the Arabian Sea to those of Gallo-Reynoso and Figueroa-Carranza (1995) around Isla da Guadalupe, Mexico.

The distinctive color patterning of the newly identified *Indopacetus* calves was compared to that of calves of these unidentified bottlenose whales observed and

Table 4. Mandibular and tooth measurements for Longman's beaked whale. Measurements were made by the authors indicated in the table, following Moore (1972). Where two measurements are given, the first is from the left hand side, and the second is from the right. E, estimate (e.g., due to uncertainty because of wear). No mandible is held for the Kenyan specimen. % ML, percentage of mandible length (based on mean where two measurements are given).

	Maldives		Queensland		Somalia		South Africa		South Africa	
	—		QM-J2106		MZUF 1956		PEM1960 ^a		PEM292 ^b	
	(Anderson, <i>this paper</i>)		(Ross, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)		(Ross, <i>this paper</i>)	
	mm	% ML	mm	% ML	mm	% ML	mm	% ML	mm	% ML
1. Length of mandible	1,075	100	1,087	100	1,010	100	626	100	—	—
2. Length of symphysis (fused length)	295	27	300	28	290	29	—	—	—	—
3. Length of symphysis (including unfused posterior part)	340	32	327	30	290	29	138.5	22	—	—
4. Height mandible at coronoid process	174/178	16	166	15	170	17	124	20	—	—
5. Outside height mandible at mid-length of alveolus	37/34	3	36	3	—	—	33	5	—	—
6. Inside height mandible at mid-length alveolus	43	4	40	4	—	—	20E	—	—	—
7. Length posterior of condyle to posterior of symphysis	775	72	773	71	745	74	486	78	—	—
8. Length posterior of condyle to posterior margin of condyle	1045/1050	97	957	88	—	—	590	94	—	—
9. Length alveolus	29/28	3	30	3	—	—	22	4	—	—
10. Width of alveolus	17/18	2	18	2	—	—	10.5	2	—	—
11. Tip of mandible to anterior margin of alveolus	3	—	6	1	—	—	5	1	—	—

Table 4. Continued.

	Maldives		Queensland		Somalia		South Africa		South Africa	
	(Anderson, <i>this paper</i>)		(Ross, <i>this paper</i>)		(Azzaroli 1968)		(Best, <i>this paper</i>)		(Ross, <i>this paper</i>)	
	mm	% ML	mm	% ML	mm	% ML	mm	% ML	mm	% ML
12. Greatest (vertical) length of tooth	36	3	—	—	—	—	27	4	20	—
13. Greatest antero/posterior width of tooth	15	1	—	—	—	—	11E	—	16	—
14. Greatest breadth of tooth perpendicular to greatest length	19	2	—	—	—	—	13	2	—	—
15. Depth of alveolus	—	—	26	2	—	—	—	—	—	—

^a Tips of mandibular rami broken but restored.

^b Based on X-ray of tooth *in situ* (Fig. 10E).

photographed at sea (see Pitman *et al.* 1999). The specific features listed by Pitman *et al.* (1999) are clearly evident in the South African specimens (Fig. 3). These include the high, white sides which are separated from the pale face and melon area by a dark band extending down from just behind the blowhole toward the flipper, and a white "ear" spot embedded within this dark band (*e.g.*, Fig. 3A this paper, circled; fig. 2C, F, Pitman *et al.* 1999). Dorsally, in both the specimens described in Pitman *et al.* (1999) and PEM292, the white of the melon extends posteriorly only as far as the blowhole. We view this matching color pattern as confirmatory evidence that the unidentified (tropical) bottlenose whale is in fact *I. pacificus* as suggested by Mörzer Bruyns (1971) and Pitman *et al.* (1999).

The dorsal fin shape of the animals pictured in Pitman *et al.* (1999) is also very similar to that of the South African specimens; falcate and pointed (Fig. 3H, I, this paper; fig. 2B, Pitman *et al.* 1999). In some individuals, the melon shape is similar to that of the Maldivian female. However, that of others is more prominent (angle with beak $\sim 90^\circ$; *e.g.*, fig. 2A, far right animal, Pitman *et al.* 1999). Assuming that dimorphism in melon shape follows a similar trend as in *Hyperoodon* spp. (*e.g.*, Mead 1989b), these latter animals may represent adult males. No erupted teeth have been observed on tropical bottlenose whales at sea (Pitman *et al.* 1999). However, some of the animals pictured in Pitman *et al.* (1999) have parallel linear scar tracks on their backs and flanks. These were likely caused by tooth rakes inflicted by conspecific males; their form is consistent with those made by a species with apical teeth. The apparent use of the teeth as "tusks" in intraspecific combat is common among beaked whales (*e.g.*, Heyning 1984).

Analyses of mtDNA sequence data presented here have confirmed the genetic distinctiveness of Longman's beaked whale. However, further phylogenetic comparisons aimed at testing the taxonomic status of the genus *Indopacetus* were inconclusive. Until fresh tissue samples become available for this species, from which long sequences from slowly evolving nuclear loci can be amplified (*i.e.*, allowing robust reconstruction of higher-level relationships among ziphiids; see Dalebout 2002), this question can be addressed only through reference to morphological features.

Moore (1968) placed Longman's beaked whale (formerly *Mesoplodon pacificus*) in the new genus, *Indopacetus*, based on four cranial characters observed in the holotype and Somali skulls, the only known specimens of this species at that time. All four of these features are also visible in the skulls of the Kenyan and South African (PEM1960) animals. Although the vertex sutures of the Maldivian specimen were not sufficiently clean for detailed examination, the rostrum form was similar to that of the other specimens. The presence of these features in all specimens of Longman's beaked whale examined to date (in particular the distinctive arrangement of the nasal and frontal bones on the vertex; *e.g.*, Fig. 9) confirms that they are indeed diagnostic for this species, as suggested by Moore (1968). A more contentious question is whether these and other characters (summarized in Table 5) distinguish Longman's beaked whale sufficiently from other ziphiids to warrant its placement in a separate genus. (Note that only features 1–4 and 7 of Table 5 distinguish *Indopacetus* from all other ziphiid genera. Tooth form and alveolus depth have yet to be knowingly examined in an adult male. Conclusions regarding body form are based on qualitative assessment only).

The statements regarding the number of ribs and fused cervical vertebrae (Table 5, features 8, 9) require discussion. Both are subject to qualification as larger sample sizes may reveal overlap with other genera. Based on the examination of three specimens, *I. pacificus* appears to have ten pairs of ribs. Eight to nine pairs of ribs have

Table 5. Summary of diagnostic morphological features for Longman's beaked whale, *Indopacetus pacificus*.

	Diagnostic features	Reference
1	On the vertex of the skull, the frontal bones occupy an area that approximates or exceeds that occupied by the nasal bones.	Moore (1968)
2	On the vertex of the skull, there is minimal extension of the premaxillary crest between the nasal and maxillary bones, or between the frontal and maxillary bones.	Moore (1968)
3	On the dorso-lateral margin of the maxillary bone above the orbit, there is a deep groove about half the length of the orbit.	Moore (1968)
4	The premaxillae, as seen in dorsal view, retain an even width to about the midlength of the rostrum, where they may expand slightly before converging again towards the tip of the rostrum.	Moore (1968)
5	Shallow alveoli (tooth sockets) compared to <i>Mesoplodon</i> . ^a	Moore (1968)
6	Comparatively simple cone-like teeth compared to most <i>Mesoplodon</i> spp. ^a	this paper
7	Depth of the rostrum at mid-length is proportionately thinner than in other ziphiid genera.	this paper
8	Ten pairs of ribs compared to <i>Hyperoodon</i> (eight or nine). ^b	this paper
9	First five cervical vertebrae fused (<i>Mesoplodon</i> , first three fused; <i>Hyperoodon</i> , all seven fused). ^b	this paper
10	Robust body form compared to <i>Mesoplodon</i> . ^c	this paper
11	Bulbous well-defined melon compared to <i>Mesoplodon</i> (but similar to <i>Tasmacetus</i>).	this paper
12	Color pattern distinct from <i>Hyperoodon</i> .	Pitman <i>et al.</i> (1999); this paper

^a However, an adult male has yet to be knowingly examined.

^b Larger sample sizes may reveal overlap in these meristic characters.

^c Based on qualitative evaluation only.

been recorded for *Hyperoodon* spp. (based on examination of eight specimens; Ross 1984, Mead 1989b), while 9–11 ribs have been recorded in *Mesoplodon* spp. (Mead 1989a). In the two specimens of *Indopacetus* for which such postcranial material was available, the first five cervical vertebrae were fused. In *Mesoplodon* and *Berardius* only the first three vertebrae are fused, comprising the atlas, axis, and third cervical (McCann 1975, Mead 1989a). In the examination of one *Tasmacetus* specimen the first six vertebrae were fused (Oliver 1937), while all seven cervical vertebrae have been recorded as fused in *Hyperoodon* (Ross 1984, Mead 1989b). Although these clear differences between genera are thought provoking, the variation observed in the genus *Ziphius* (four fused cervical vertebrae observed in five specimens, and three and six fused cervicals, respectively, observed in two other specimens; Omura 1972) suggests that caution should be taken in interpretation of these patterns. More information on the lesser-known ziphiid genera is clearly needed.

There appear to be three options regarding the systematic relationship of

Longman's beaked whale to other ziphiids: Longman's beaked whale represents either a morphologically divergent form of *Mesoplodon* (Longman 1926, Mead 1989a) convergent on *Hyperoodon* in size and shape, a tropical form of *Hyperoodon*, or a distinct genus (Moore 1968). In addition to the features of the skull and alveoli identified by Moore (1968), five characters distinguish this species from most or all *Mesoplodon* spp. (Table 5). These are the depth of the rostrum, melon form (bulbous and well defined), depth of the alveoli (shallow), tooth morphology (relatively simple and conelike, at least in adult females), and body form (robust). In external morphology, Longman's beaked whale is similar to *Hyperoodon*. Shared features include a large bulbous melon, conspicuous blow (Pitman *et al.* 1999), apical teeth, a similar color pattern (especially in juveniles), and robust body form. The ontogeny of coloration is also similar, with the contrasting pale melon of neonates in both species (Fig. 3, 4) becoming less conspicuous with age. In general, the opposite trend is seen in *Mesoplodon* spp., with color patterning, where it exists, tending to become more conspicuous with age. (Note, however, that *Mesoplodon* calves may also have pale melons). However, this species is distinguished from those of the genus *Hyperoodon* by features of the cranial morphology (Fig. 9), including the width/depth ratio of the rostrum at mid-length (Fig. 8) and potentially in the number of ribs and fused cervical vertebrae (Table 5).

To date there has been no cladistic analysis of morphological features in this family. Although clearly of value, there is also no guarantee that such an analysis would be successful due to the low sample size and ambiguous morphology of many ziphiid species. In the absence of such morphological analyses, the polarity of different character states is difficult to determine. The lack of objective criteria in taxonomy as to how different a species must be from other related species to be considered a distinct genus is also problematic. At present, however, we see no reason on morphological grounds to overturn Moore's (1968) proposal that Longman's beaked whale is sufficiently distinct from other ziphiids to be afforded its own genus, *Indopacetus*.

Although *I. pacificus* is morphologically distinct from other ziphiid species, significant potential remains for the misidentification of these animals, both at sea and when stranded. This is due in part to its rarity, remote distribution, and similarity in external form to *H. planifrons* (the same reasons this species remained unrecognized for so long, Pitman *et al.* 1999), as well the overall subtlety of diagnostic features in ziphiids. Therefore, we recommend that, as well as voucher skeletal material, tissue samples, including skin biopsy samples of animals at sea, should be collected for genetic analysis wherever possible to allow confirmation of species identity. Important information regarding comparative genetic diversity, population structure, and geographic differentiation could also be obtained from such analyses.

The discovery of these four new specimens has extended the known range of Longman's beaked whale and led to the description of its external appearance for the first time. As this species is now known from six specimens, the title of the world's rarest whale must pass to the spade-toothed whale, *M. traversii* (= *M. bahamondi*), which to date is known from only three specimens (two crania and one mandible with teeth, van Helden *et al.* 2002).

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APPENDIX

DNA Amplification

MtDNA control region primers—M13-Dlp1.5-L (5'-TGTAACGACGGCCAGT-TCACCCAAAGCTGRARTTCTA- 3'; Dalebout *et al.* 1998); Dlp5-H (5'-CCATCGW GATGTCTTATTTAAGRGGAA- 3'; Dalebout *et al.* 1998); Dlp4-H (5' -GCGGGWTRYTG RTTTCACG- 3'; C. S. Baker, unpublished); Dlp10-L (5'-CCACAG-TACTATGTCCGTATT- 3'; Baker *et al.* 1993). Product sizes (beaked whales): M13-Dlp1.5-L and Dlp5-H, ~500 bp; M13-Dlp1.5-L and Dlp4-H, ~350 bp; Dlp10-L and Dlp4-H, ~280 bp.

MtDNA cytochrome b primers—CB1-L (5' -CCATCCAACATCTCAGCATGATGAAA- 3'; Palumbi 1996); CB2-H (5' -CCCTCAGAATGATATTTGTCCTCA- 3'; Palumbi 1996); CYBMF-L (5'-GAACTATAAGAACA CTAATGACCAA- 3'; Dalebout 2002). CYBMR-H (5' -TGATTCAGCCATAGTTAACGTCTCGAC- 3'; Dalebout 2002). Product sizes: CB1-L and CB2-H, ~300 bp; CYBMF-L and CYBMF-H, ~230 bp. The latter two primers are beaked whale specific and were designed to avoid amplification of modern human mtDNA, a frequent contaminant of historic skeletal material.

PCR amplification and sequencing followed standard protocols (Palumbi 1996), except for the addition of bovine serum albumin (BSA) solution (0.5–1 µg/µl) to help overcome the effect of the inhibiting substances that often accumulate in historical material (Pääbo 1990). For both loci, amplification of the larger fragment was attempted first, which if unsuccessful, was followed by attempts to amplify successively smaller fragments. These shorter fragments nest within the larger fragment characterized for each locus. A primer map is available from the website, <http://www.DNA-surveillance.auckland.ac.nz>.

Phylogenetic Analyses

Neighbour-joining—Kimura 2-parameter corrected distance, gamma shape parameter = 0.5; Missing sites and gaps ignored for affected pairwise comparisons; 1,000 neighbour-joining bootstrap replicates.

Maximum parsimony—Heuristic search with sub-tree pruning-regrafting (SPR) branch swapping and random sequence addition, 10 replicates. Control region, nine trees found (consistency index [CI], 0.405; retention index [RI], 0.748); cytochrome *b*, 122 trees found (CI, 0.405; RI, 0.748); 10,000 fast heuristic bootstrap replicates.

Maximum likelihood—All starting parameters for an HKY85+G+I model of sequence evolution (different rates for transition and transversion substitutions, unequal base composition, substitution rates vary among sites, some sites invariant) were estimated from neighbour-joining trees. Heuristic search with SPR branch swapping and random sequence addition, 10 replicates; 200 fast heuristic bootstrap replicates.