

A NEW SPECIES OF BEAKED WHALE
MESOPLODON PERRINI SP. N.
(CETACEA: ZIPHIIDAE) DISCOVERED
THROUGH PHYLOGENETIC ANALYSES OF
MITOCHONDRIAL DNA SEQUENCES

MEREL L. DALEBOUT

School of Biological Sciences, University of Auckland,
Private Bag 92019, Auckland 1000, New Zealand
E-mail: m.dalebout@auckland.ac.nz

JAMES G. MEAD

National Museum of Natural History, Mailstop NHB 108,
Smithsonian Institution, Washington, DC 20560, U.S.A.

C. SCOTT BAKER¹

School of Biological Sciences, University of Auckland,
Private Bag 92019, Auckland 1000, New Zealand

ALAN N. BAKER

Science & Research Unit, Department of Conservation,
P. O. Box 10-420, Wellington, New Zealand

ANTON L. VAN HELDEN

Museum of New Zealand Te Papa Tongarewa,
P. O. Box 467, Wellington, New Zealand

ABSTRACT

Mesoplodon perrini, a new species of beaked whale is described on the basis of five animals stranded on the coast of California (between 32°55'N, 117°15'W and 36°37'N, 121°55'W) from May 1975 to September 1997. Four of these animals were initially identified as Hector's beaked whales *M. bectori* based on cranial morphology (Mead 1981). A fifth specimen was initially identified as a neonate Cuvier's beaked whale *Ziphius cavirostris* based on external features. These specimens were first recognized as representatives of an undescribed species through phylogenetic analysis of mitochondrial (mt) DNA control region and cytochrome *b* sequence data. Although similar morphologically, the genetic data do not support a close evolutionary relationship between *M. perrini* and *M. bectori*. Instead, these data suggest a possible sister-

¹ Corresponding author; e-mail: cs.baker@auckland.ac.nz.

species relationship with the lesser beaked whale *M. peruvianus*. Sightings of two small beaked whales off California in the 1970s which were tentatively identified as *M. hectori* are also likely to be *M. perrini*. We suggest that *M. hectori* is confined to the Southern Hemisphere, while *M. perrini* is known to date only from the North Pacific.

Key words: molecular genetics and systematics, morphology, external appearance, natural history, distribution, *Mesoplodon perrini*, Perrin's beaked whale.

Beaked whales (Cetacea: Ziphiidae) are the least known of all cetacean families. In terms of species diversity, they are second only to oceanic dolphins (Family Delphinidae), with 20 species currently recognized. Beaked whales are rarely observed at sea due to their preference for deep ocean waters and elusive habits. Most species are known from only a small number of stranded specimens, and several have never been seen alive. Of the twelve cetacean species described in the last 100 years, eight have been ziphiids, primarily of the genus *Mesoplodon*. In the closing decade of the 20th century, two new beaked whales were discovered; the lesser beaked whale *M. peruvianus* (Reyes *et al.* 1991), and Bahamonde's beaked whale *M. bahamondi* (Reyes *et al.* 1995), although the latter is now recognized as synonymous with *M. traversii* (Gray, 1874) (van Helden *et al.* 2002).

Here we document the occurrence and characteristics of a previously undescribed species of *Mesoplodon* beaked whale in the North Pacific Ocean. In the mid to late 1970s, four beaked whales stranded within 85 km of each other along the southern coast of California (Table 1). These animals were identified as Hector's beaked whales *M. hectori*, the first and only records of this species from the Northern Hemisphere (Mead 1981). In 1997 a database of mitochondrial (mt) DNA control region reference sequences was compiled to assist in beaked whale species identification (Dalebout *et al.* 1998, Henshaw *et al.* 1997). All specimens in this reference database were validated through examination by experts in cetacean morphology and the collection of diagnostic skeletal material or photographic records (Dizon *et al.* 2000). Among the specimens incorporated in these analyses was one of the "*M. hectori*" from California (USNM504259; Henshaw *et al.* 1997). A phylogenetic review of the database, which at this time consisted of reference sequences from 16 of the 20 described species, including Southern Hemisphere *M. hectori*, suggested that the California specimen was not of this species nor any other species in the database (Dalebout *et al.* 1998).

To further investigate this anomaly, DNA was extracted from the remaining three specimens from California described by Mead (1981). Phylogenetic analyses of mtDNA control region and cytochrome *b* sequences from these specimens, using a complete reference database which now includes all 20 described beaked whale species, confirmed that all four were of the same species, yet did not represent *M. hectori* nor any other known ziphiid species (Dalebout 2002). Instead, these results suggested that the California specimens represented an undescribed species of beaked whale. Here we present a formal description of this new species, and include a description of a fifth specimen,

Table 1. Specimens of *Mesoplodon perrini* from California, in order by stranding date. Total length in cm.

Museum number	Field number	Date found	Locality	Coordinates	Total length	Sex
USNM504259	—	1975 May 22	Camp Pendleton	33°15'N, 117°26'W	210	M
USNM504260	—	1975 May 28	Camp Pendleton	33°16'N, 117°26'W	443	F
USNM504853	—	1978 Sept 9	Carlsbad	33°07'N, 117°20'W	390	M
LAM088901	JRH 052	1979 Dec 27	Torrey Pines State Reserve	32°55'N, 117°15'W	245	M
—	TMMC-C75	1997 Sept 18	Monterey	36°37'N, 121°55'W	224	M

which stranded in Monterey, California, in 1997, and was initially identified as a neonate Cuvier's beaked whale *Ziphius cavirostris* from external morphology.

METHODS

Material Examined

Five specimens of the undescribed species from California were examined (Table 1). Phylogenetic analyses of mtDNA control region and cytochrome *b* sequences were used to compare these specimens to all 20 previously described ziphiid species.

Museums and institutions holding specimens of the new species are as follows: Los Angeles County Museum of Natural History, California (LAM) and the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Tissue samples are held by: the School of Biological Sciences, University of Auckland, New Zealand (AUNZ); Southwest Fisheries Science Centre, La Jolla, CA (SWFSC); and, The Marine Mammal Centre, Sausalito, CA (TMMC).

Morphological comparisons were made to 12 specimens of *M. hectori* held by the following museums: Museum of New Zealand Te Papa Tongarewa (NMNZ), $n = 7$; The Australian Museum, Sydney (AMS), $n = 1$; Tasmanian Museum and Art Gallery (TAM), $n = 1$; the South Australian Museum (SAM), $n = 1$; and, Museo Acatashún de Aves y Mamíferos Australes (MAAMA), Tierra del Fuego, $n = 2$. Further information on specimens of *M. hectori* examined can be obtained from JGM or AVH.

DNA Extraction and Sequencing

DNA was extracted from the teeth and cartilage on the museum-held material of the four specimens (USNM504259, USNM504260, USNM504853, LAM088901) described by Mead (1981), using the silica-based method of Höss and Pääbo (1993), as modified by Matisoo-Smith *et al.* (1997), and techniques described in Pichler *et al.* (2001). Museum material from USNM504259 was included to confirm that the original soft tissue sample (SWFSC-z4976) used by Henshaw *et al.* (1997) had indeed been derived from this specimen. (Soft tissue samples were not available for the other three specimens). Total genomic DNA was extracted from soft tissue samples obtained from the Monterey specimen (TMMC-C75) using standard methods (Sambrook *et al.* 1989), as modified by Baker *et al.* (1993). Samples were stored in salt-saturated, dimethylsulphoxide (DMSO) solution prior to analysis.

Segments of the 5' end of the mtDNA control region and 5' end of the cytochrome *b* gene were amplified and sequenced from all five specimens, and aligned to the sequences already in the beaked whale reference database, as described in Dalebout (2002).

Phylogenetic Analyses

Phylogenetic relationships among the California specimens and the 20 known beaked whale species were reconstructed from sequence data from both mtDNA loci using maximum likelihood (ML) methods (consensus length of alignments, control region, 437 bp; cytochrome *b*, 384 bp; Dalebout 2002). Baird's beaked whale, *Berardius bairdii*, which likely represents the most basal extant species in this family (*e.g.*, Dalebout *et al.* 1998) was used as an out-group.

To further investigate sister-species relationships among a subset of *Mesoplodon* species, including the California specimens, the control region and cytochrome *b* sequences were combined to increase phylogenetic signal (consensus length of alignment, 821 bp). A partition-homogeneity test (Farris *et al.* 1995) indicated that these loci were congruent (branch and bound search, 1,000 replicates). Although the individuals representing each species differed between the two loci in some cases, this was not considered a problem as intraspecific variation was generally much lower than interspecific variation (see discussion below). Starting parameters for ML reconstruction were estimated from an initial neighbour-joining tree built using general-time-reversible (GTR) distances. For ML analyses, the heuristic search option, with random sequence addition (100 replicates), and sub-tree pruning-regrafting branch swapping, was used. The statistical consistency of groupings was evaluated by 200 ML bootstrap resamplings of the data. Bremer support was calculated using TreeRot v.2a (Sorensen 1999), based on one of the three most parsimonious trees (= ML tree) obtained through an exhaustive parsimony search. All phylogenetic analyses were conducted using the program PAUP* 4.0 beta 6 (Swofford 1999).

RESULTS

DNA Sequence Data

For the mtDNA control region, fragments ranging in length from 245 bp to 434 bp were sequenced successfully from the five California specimens. For the mtDNA cytochrome *b*, fragments ranging in length from 276 bp to 384 bp were sequenced successfully. For those specimens represented by hard tissue (*i.e.*, tooth or cartilage; USNM504260, USNM504853, LAM088901), only shorter fragments were obtained, as expected from DNA extractions from such material (Höss and Pääbo 1993). Comparison of the mtDNA control region sequence published by Henshaw *et al.* (1997) (Genbank Accession No. U70466) with that obtained from museum-held material from USNM504259 confirmed that they were identical, and as such likely derived from the same specimen. All previously unpublished sequences have been deposited in Genbank (Accession No.'s: AF441254–AF441263).

Phylogenetic Analyses

Phylogenetic analyses of sequence data from the mtDNA control region (Fig. 1) and cytochrome *b* (not shown) confirmed that all five California specimens were of the same species, and distinct from all other 20 known species of beaked whale. Although higher-level relationships were not well resolved by these rapidly evolving mtDNA loci (*i.e.*, bootstrap scores for most internal nodes, <50%), all species-specific groupings were supported by high bootstrap scores (>80%). MtDNA control region sequences representing the southern bottlenose whale *Hyperoodon planifrons* were the exception to this trend.

To further investigate the genetic distinctiveness of the California animals, and exclude the possibility that they represent only a highly divergent, geographic subdivision of *M. hectori*, we compared the combined control region and cytochrome *b* sequences (821 bp) to a subset of potential sister-taxa (Fig. 1, gray box). While a monophyletic grouping of the California animals and *M. hectori* would argue for a single-species classification despite a deep divergence (Lento *et al.* 1997, Wayne *et al.* 1990), the results indicated instead that the California specimens were more closely related to at least four other species of *Mesoplodon*, than to the morphologically similar *M. hectori* (bootstrap score, 83%; Bremer support = 7; Fig. 2). No synapomorphies were found to unite the California specimens and *M. hectori* exclusive of other beaked whales. These results allowed us to reject the hypothesis of a deep intraspecific divergence, and argue instead that these specimens represent a previously unrecognized species of beaked whale.

Although higher-level relationships among this subset of *Mesoplodon* species were not fully resolved (Fig. 2), there was some support for a sister-species relationship between the California specimens and the lesser beaked whale *M. peruvianus* (bootstrap score, 69%). There was also low-level support for a clade consisting of these two species, plus Gray's beaked whale *M. grayi*, (bootstrap score, 55%). Phylogenetic reconstructions based on nuclear sequences support a similar pattern of relationships among these species (Dalebout 2002).

Intra- and Interspecific Genetic Divergence

Over the 245 bp fragment of the mtDNA control region covered by sequence data from all five specimens, all shared the same haplotype (Fig. 3). Analysis of the 280 bp fragment of the cytochrome *b* covered by all five specimens revealed two variable sites (one synonymous third position transversion and one non-synonymous first position transition) defining three unique haplotypes (Fig. 4). The adult female (USNM504260), and two of the three calves (USNM504259 and TMMC-C75) share the same haplotype at this locus, while the adult male (USNM504853) and the remaining calf (LAM088901) were both unique. The adult female and the calf, USNM504259, both stranded at Camp Pendleton in the same week of May 1975 (Table 1).

Comparisons of intra- and interspecific pairwise sequence divergence for all

20 beaked whale species confirmed that the California specimens follow a similar pattern to other ziphiids (Fig. 5a, b). Over the 437 bp control region alignment, intraspecific variation (using two representatives per species) was found to be generally less than 2%, while interspecific variation was generally greater than 4%. Similar trends were found in a previous analysis, which compared intra- and interspecific genetic divergence among nine described beaked whale species (Dalebout *et al.* 1998). The new species differs from all other beaked whales by an average of 8.55% over this fragment. Over the 384 bp mtDNA cytochrome *b* alignment, intraspecific variation was found to be generally less than 1.5%, while interspecific variation was found to be generally greater than 3% for 20 described beaked whale species. The new species differs from all other beaked whale species by an average of 15.24% over this fragment. See Dalebout (2002) for discussion regarding comparative levels of divergence at the mtDNA cytochrome *b* versus the control region among the Ziphiidae.

DESCRIPTION

Order Cetacea Brisson, 1762

Family Ziphiidae Gray, 1865

Mesoplodon perrini sp. n.

HOLOTYPE

Adult male (USNM504853); skull, mandible, and postcranial skeleton, at the National Museum of Natural History, Smithsonian Institution, Washington, DC. This specimen was found on 9 September 1978, by G. Carsten, and collected two days later by J.G.M.

TYPE LOCALITY

Carlsbad, California (33°07'N, 117°20'W), United States of America.

PARATYPES

Male calf (USNM504259); fragmented cranium and postcranial skeleton, at the Smithsonian National Museum of Natural History, Washington, DC, collected by W. F. Perrin.

Adult female (USNM504260); skull, mandible, and postcranial skeleton, at the Smithsonian National Museum of Natural History, Washington, DC, collected by W. F. Perrin.

Male calf (LAM088901); skull, mandible, at the Los Angeles County Museum of Natural History, collected by J. R. Henderson (JRH 052).

Male calf (TMMC-C75); skull, mandible, and postcranial skeleton, at the Los Angeles County Museum of Natural History, collected by M. Haulena.

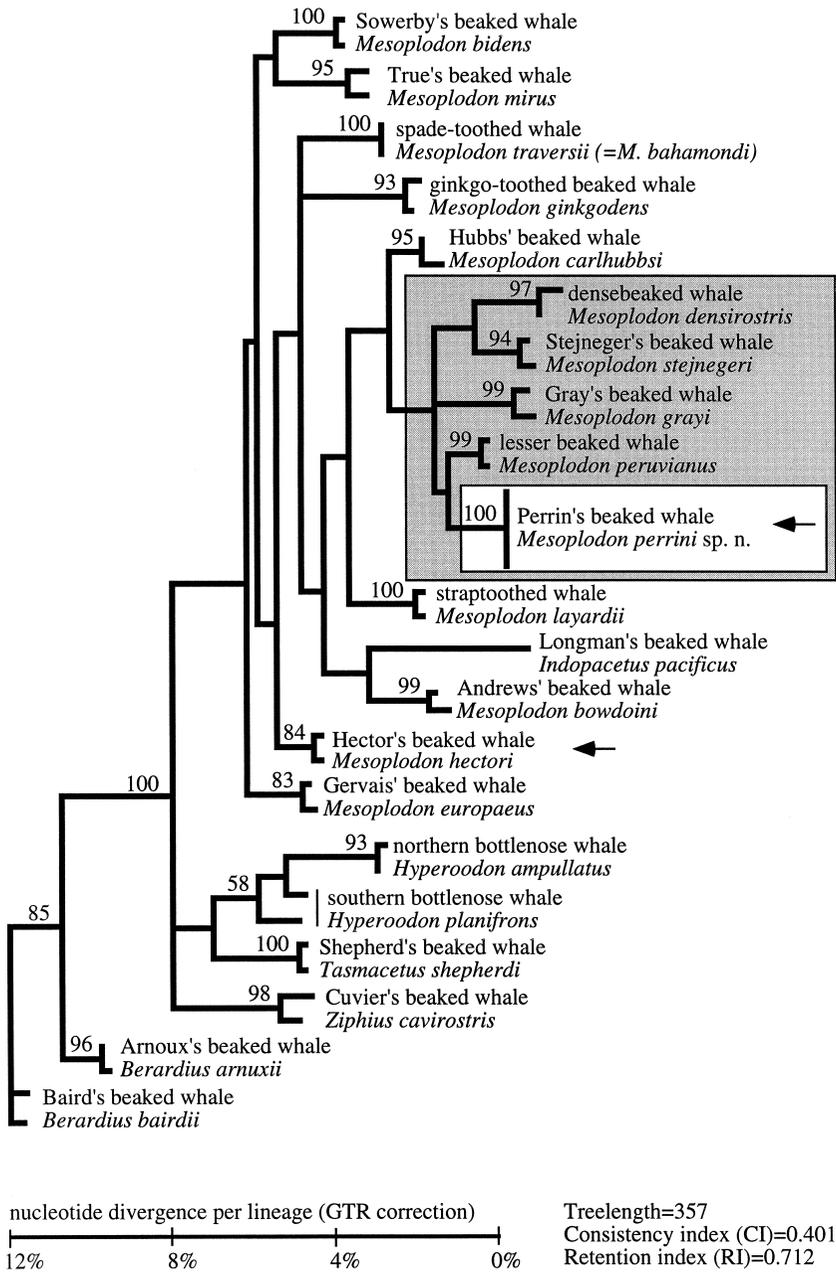


Figure 1. Phylogenetic relationships among the 20 described species of beaked whales (Ziphiidae) from maximum-likelihood analyses, based on 437 bp of mitochondrial DNA control region. Numbers above internal nodes indicate bootstrap values $\geq 50\%$. All described species represented by two reference specimens where possible. Arrows highlight respective positions of *Mesoplodon perrini* sp. n. and *M. hectori*, the species as which several specimens of this new species were initially described. Gray box indicates subset of taxa, with addition of *M. hectori*, used in further analyses. Note

ETYMOLOGY

The specific name, *perrini*, was chosen as a tribute to the American cetacean biologist, Dr. W. F. Perrin, for his role in the collection of two of the known specimens of this species, and his ongoing contribution to marine mammal science and conservation. We propose this species be known by the common name, Perrin's beaked whale.

DIAGNOSIS

Molecular Characters

M. perrini can be differentiated from all other species of *Mesoplodon* beaked whales based on molecular genetic characters, as demonstrated by phylogenetic analyses of mtDNA control region and cytochrome *b* sequences (Fig. 1–5). Over the 434 bp control region segment, *M. perrini* is distinguished from *M. hectori* by 26 diagnostic sites (5.99% pairwise sequence divergence), including two insertion-deletions (indels), and from *M. peruvianus*, its likely sister-species, by 16 diagnostic sites (3.46%), including one indel (Fig. 3). Over the 384 bp cytochrome *b* segment, *M. perrini* is distinguished from *M. hectori* by 37 diagnostic sites (9.64%), including four first position and three second position substitutions, and from *M. peruvianus* by 48 diagnostic sites (12.50%), including six first position and four second position substitutions (Fig. 4). In comparisons including all ziphiid species, *M. perrini* is distinguished by one diagnostic site (*sensu* Davis and Nixon, 1992) at the control region (position 111 = A; Fig. 3), and one diagnostic site at the cytochrome *b* (position 182 [2nd] = T; Fig. 4), given a mean of two diagnostic sites per species for both fragments. Note that high levels of homoplasy were observed at these mtDNA loci due to the rapid rate of accumulation of mutations and the large number of species to be differentiated (Sanderson and Donoghue 1989).

Morphological Characters

The following characters of the mandibles, teeth, and skull are, when combined, diagnostic for *M. perrini*:

- (1) Short mandibular symphysis (19%–23% mandible length).
- (2) Convex profile to anterior part of mandible over the length of the symphysis.

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that *M. bahamondi* (Reyes *et al.* 1995) was recently recognized as synonymous with *M. traversii*, a species described by J. E. Gray in 1874 (van Helden *et al.* 2002). The aligned sequence files used in these analyses are available electronically from http://www.sbs.auckland.ac.nz/research_groups/ecology_and_evolution/molecular_ecol_evo_lab or <http://www.dna-surveillance.auckland.ac.nz>.

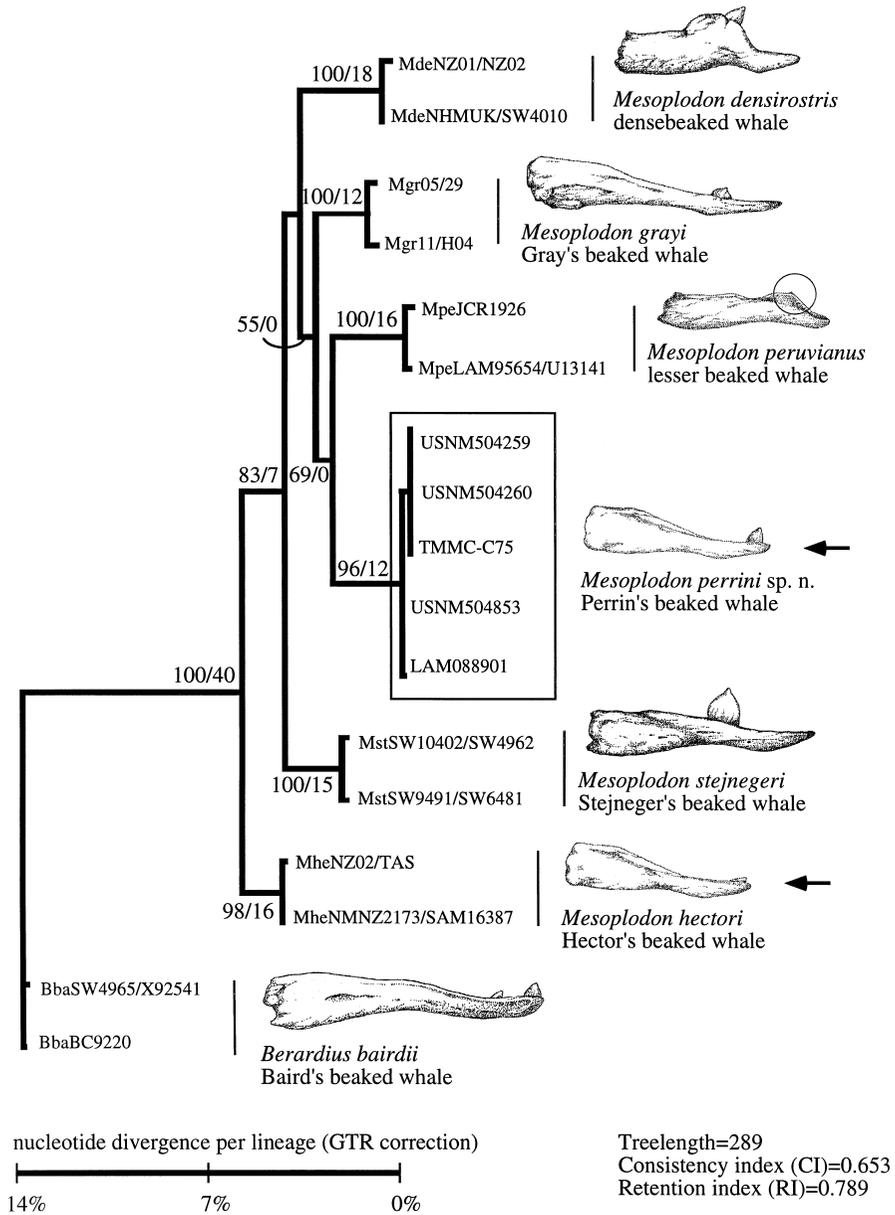


Figure 2. Phylogenetic relationships among *Mesoplodon perrini*, *M. hectori*, and subset of related *Mesoplodon* beaked whales, based on maximum likelihood (ML) analyses, using combined mitochondrial DNA control region and cytochrome *b* sequences (821 bp). Numbers adjacent to internal nodes are ML bootstrap values $\geq 50\%$ /Bremer support indices. The figures adjacent to the branch termini show the diagnostic size, shape, and position of the teeth in the lower jaw of the adult male of each species. The circle indicates the position of the diminutive tooth in *M. peruvianus*. The arrows draw attention to the morphological similarity between *M. perrini* and *M. hectori*.

- (3) Sub-terminal narrow teeth, up to 64 mm long, 47 mm wide and 12 mm broad, with smooth anterior margins and a 60°–70° terminal angle.
- (4) Narrow triangular subvertex.
- (5) Narrow, reverse V-shaped space between right and left nasals.
- (6) Narrow premaxillaries adjacent to the antorbital notches.
- (7) Small, but distinct basirostral groove.
- (8) Antorbital notches and prominences formed by the maxilla.
- (9) Margins of the posteromedial portion of the maxillaries angled sharply laterally.

MORPHOLOGICAL DESCRIPTION

Osteology and Dentition

Cranial and mandibular measurements are shown in Table 2, 3, respectively. The premaxillary crest is relatively narrow and conservative in shape (Fig. 6), similar to that of *M. hectori* and *M. peruvianus*. The cranium of the holotype is not greatly inflated, adding to the narrow triangular appearance of the synvertex, which is constricted laterally at the confluence of the maxillaries with the supraoccipitals. The margins of the posteromedial portion of the maxillaries (posterior to the synvertex) are angled sharply laterally, more so on the right side, and the sides of the cranium are steep. There are moderately formed maxillary crests above the orbits. The rostrum is relatively short (82%–93% zygomatic width [ZW]) for a *Mesoplodon*, and the mesorostral canal is fully ossified in the adult male. The mandibles have a short symphysis, the ventral profile of which is convex. The remaining ventral profile of the mandible is concave and then convex again near the posterior end. As in other species of this genus, the teeth are reduced to a single, laterally compressed pair in the mandible. The teeth are set close to the apex of the jaw, and are thus completely anterior to the posterior end of the symphysis. In the adult male holotype specimen, the anterior edge of the teeth is 23 mm from the tip of the lower jaw in life, with 33 mm of the tooth exposed above the gumline. The shape of the exposed portion of the tooth is a rough isosceles triangle, but with a smoothly convex anterior margin. The teeth have a sharp terminal angle of between 60° and 70°, and splay outwards from the perpendicular by an angle of approximately 15° (Fig. 7, 8e). The teeth of the adult female (USNM504260) are sharply triangular, and are not erupted.

Vertebral counts, based on the four type specimens are as follows: cervicals 7 (1 and 2 fused), thoracic 9–10, lumbar 11–13, total 46–50. The phalangeal formula (based on two specimens) is I-2, II-6, III-7, IV-5, V-3 or 4.

COMPARISONS WITH *MESOPLODON HECTORI*

From the original misidentification of four of the five specimens of *M. perrini* known to date (Mead 1981, Mead and Baker 1987), it is clear that this species resembles *M. hectori* (Gray, 1871) morphologically. Further examination of the

	10	20	30	40	50	60
TMMC-C75	GAAAAAGTCT	TGTTATAGAA	TCACCATAAC	CTTACAGTAC	TACGTCAGTA	TTGAAAAAGA
USNM504259
USNM504260	??????????	??????????	??????????	??????????	??????????	??...
USNM504853	??????????	??????????	??????????	??????????	??????????	??...
LAM088901	??????????	??????????	??????????	??????????	??????????	??...
<u>MheNMNZ2173</u>CT.	.A..G.....C...	.C.....	.T.....-
MpeLAM95654C...A.....
	70	80	90	100	110	120
TMMC-C75	AATACCCTAC	AGTACATTTA	CTGTATTAAT	CATACAGACA	CATTCA-CTG	AGCGCTAATA
USNM504259
USNM504260
USNM504853
LAM088901
<u>MheNMNZ2173</u>	...T.T...A...	..CC..C..A	GA.A.....
MpeLAM95654	A.....	..CC..C..A	G.....
	130	140	150	160	170	180
TMMC-C75	TATAGCGTCT	CTCTAAAAGT	GTATGTATAT	ATATACTATG	TATAACTGIG	CATTACATTTA
USNM504259
USNM504260
USNM504853
LAM088901
<u>MheNMNZ2173</u>TC.G..C.G.
MpeLAM95654C.GG...GT...
	190	200	210	220	230	240
TMMC-C75	TTTTCACTAC	GGAGAGTTAA	AGCTCGTAAT	TAATTTTTTT	TATTTTACAT	AAGTACATAA
USNM504259
USNM504260
USNM504853
LAM088901
<u>MheNMNZ2173</u>
MpeLAM95654	A.....
	250	260	270	280	290	300
TMMC-C75	TTTGCACTAT	TCGTACATGT	GCCCCTTCCA	TTAGATCAGC	AGCTTAATCA	CCATGCCGCG
USNM504259
USNM504260??
USNM504853
LAM088901??
<u>MheNMNZ2173</u>A
MpeLAM95654
	310	320	330	340	350	360
TMMC-C75	TGAAACCAGC	AACCCGCTTG	GCAGGGATCC	CTCTTCTCGC	ACCGGGCCCA	TCGATCGTGG
USNM504259
USNM504260	??????????	??????????	??????????	??????????	??????????	??????????
USNM504853
LAM088901	??????????	??????????	??????????	??????????	??????????	??????????
<u>MheNMNZ2173</u>
MpeLAM95654A.....
	370	380	390	400	410	420
TMMC-C75	GGGTAGCTAA	TATTCGCTTT	TATAAGACAT	CTGGTTCTTA	CTTCAGGACC	ATCTTAACTT
USNM504259	...??????	??????????	??????????	??????????	??????????	??????????
USNM504260	??????????	??????????	??????????	??????????	??????????	??????????
USNM504853
LAM088901	??????????	??????????	??????????	??????????	??????????	??????????
<u>MheNMNZ2173</u>C.....T.....
MpeLAM95654T.....
	430					
TMMC-C75	AAAATCGCCC	ACTC				
USNM504259	??????????	?????				
USNM504260	??????????	?????				
USNM504853				
LAM088901	??????????	?????				
<u>MheNMNZ2173</u>				
MpeLAM95654				

mandibles, teeth and skulls of *M. perrini* and *M. hectori*, including new material from the latter species held in Southern Hemisphere museum collections, show distinctive differences between the two species. These differences are documented below.

Mandibles and Teeth

The mandibles of *M. perrini* have a short symphysis (19.3%–23.2% of mandible length) compared to *M. hectori* (25.9%–33.8% of mandible length). The ventral lateral outline of the rami is convex over the length of the symphysis in *M. perrini*, whereas in *M. hectori* this outline is concave (Fig. 9). The entire ventral margin of the *M. hectori* mandible consists therefore of two concave areas, giving the rami a more slender appearance. This characteristic mandible shape in *M. hectori* was noted by Harmer (1924).

In specimens of *M. perrini*, the teeth are situated slightly posterior (1–2 cm) to the tip of the mandibles. In *M. hectori*, this is only the case in juvenile and sub-adult specimens; the fully adult male teeth are situated at the very tip of the mandibles. In *M. perrini*, the alveoli are only slightly expanded to take the teeth, which reach 12 mm in breadth in adult males, giving the jaw an smoothly attenuating tip. In *M. hectori*, the adult male teeth are broader (<17.5 mm) and the alveoli are consequently expanded, such that the tip of the jaw is swollen.

There are small differences in the teeth of these species. The teeth in *M. perrini* have, in profile, a smoothly convex anterior margin, whereas those of *M. hectori* have a margin with three flattish areas between the denticle and root (Fig. 10). In subadult specimens of *M. hectori*, these “flats” are more defined and appear as steps in the margin. *In situ*, the teeth of *M. perrini* are more erect, with a shorter posterior margin than those of *M. hectori*. The angle formed by the denticle is 60°–65° in *M. perrini* and 85°–90° in *M. hectori*. The female teeth of *M. perrini* are thin and sharply triangular with straight or slightly concave margins, while those of *M. hectori* have the same flat areas in the anterior margin as do the males of that species.

Cranial Morphology

The main difference in cranial morphology between these two species is in the shape of the neurocranium and synvertex. In *M. perrini*, the synvertex

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Figure 3. Aligned sequences for *Mesoplodon perrini* over 434 bp of mitochondrial DNA control region. Identity to reference sequence, TMMC-C75, indicated by dots. All five specimens of *M. perrini* share same haplotype over this fragment. Sequences from *M. hectori* MheNMNZ2173 (underlined) and *M. peruvianus* MpeLAM95654 included for comparison. Position 1 of alignment corresponds to position 15891 of fin whale, *Balaenoptera physalus*, mtDNA genome (Arnason *et al.* 1991). Diagnostic nucleotide position distinguishing *M. perrini* from all 20 previously described species of beaked whales at this locus highlighted in gray.

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                10          20          30          40          50
TMMC-C75      ATG ATC AAC ATT CGA AAA ACA CAC CCA TTA ATA AAA ATT ATC AAC AAC GCA TTT
USNM504259    ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
USNM504260    ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
USNM504853    ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
LAM088901     ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
MheSAM16387  ... .C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.
Mpe-U13141    ... .C. ... ..T. ... ..T. ... ..C.G ... ..C.G ... ..C.G ... ..T. ... ..T.

                60          70          80          90          100
TMMC-C75      ATT GAT CTT CCC ACT CCA TCA AAC ATC TCC TCA TGA TGA AAC TTT GGT TCA TTA
USNM504259    ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
USNM504260    ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
USNM504853    ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
LAM088901     ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ??? ???
MheSAM16387  ... ..C. ... ..C. ... ..T. ... ..T. ... ..T. ... ..T. ... ..C. ... ..C.
Mpe-U13141    ..C ... ..T ..C ..G ... ..T ... ..T ... ..C ... ..C ... ..C ... ..C ..C ..C.

                110         120         130         140         150         160
TMMC-C75      CTC GGT CTC TGC CTA ATC ATA CAA ATT CTT ACA GGC TTA TTC CTA GCA ATA CAC
USNM504259    ... ..C. ... ..C.
USNM504260    ... ..C. ... ..C.
USNM504853    ??? ??? ??? ??? ? ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.
LAM088901     ... ..C. ... ..C.
MheSAM16387  ... ..C. ... ..G. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.
Mpe-U13141    ... ..C. ... ..T. ... ..T. ... ..C. ... ..C. ... ..C. ... ..T. ... ..T.

                170         180         190         200         210
TMMC-C75      TAC ACA CCA GAC ACT ACA ATA GCC TTT TCA TCA GTT GCA CAC ATC TGC CGA GAC
USNM504259    ... ..C. ... ..C.
USNM504260    ... ..C. ... ..C.
USNM504853    ... ..C. ... ..C.
LAM088901     ... ..C. ... ..C.
MheSAM16387  ... ..C. ... ..A. ... ..C. ... ..C. ... ..C. ... ..C. ... ..A. ... ..T. ... ..T.
Mpe-U13141    ..T ... ..C. ... ..C. ... ..C. ... ..C. ... ..G. ... ..Y. AT. ... ..T. ... ..T.

                220         230         240         250         260         270
TMMC-C75      GTT AAC TAT GGT TGA ATT ATC CGA TAC CTA CAT GCA AAT GGA GCT TCC ATA TTT
USNM504259    ... ..C. ... ..C.
USNM504260    ... ..C. ... ..C.
USNM504853    ... ..C. ... ..C.
LAM088901     ... ..C. ... ..C.
MheSAM16387  ..C ..T ..C ..C ... ..C. ... ..T. ... ..C. ... ..C. ... ..C. ... ..T. ..G ..C
Mpe-U13141    ... ..T ... ..C ... ..C ... ..T ... ..T ... ..C ... ..C ... ..C ... ..C ..C ..C

                280         290         300         310         320
TMMC-C75      TTT ATC TGC CTT TAC GCA CAC ATT GGA CGC GGT CTA TAT TAC GGC TCT TAT ATT
USNM504259    ... ..C. ... ..C.
USNM504260    ... ..C. ... ..C.
USNM504853    ... ..C. ... ..C.
LAM088901     ... ..C. ... ..C.
MheSAM16387  ... ..C. ... ..C. ... ..C. ... ..C. ... ..T. ... ..C. ... ..C. ... ..C. ... ..C.
Mpe-U13141    ... ..C. ... ..C. ... ..T. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.

                330         340         350         360         370
TMMC-C75      TTT CAA AAA ACA TGA AAT ATT GGA GTA ATT TTA CTC TTC ATA GTT ATA GCT ACT
USNM504259    ... ..C. ... ..C.
USNM504260    ... ..C. ... ..C.
USNM504853    ... ..G. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.
LAM088901     ... ..G. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.
MheSAM16387  ..C ..G. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C.
Mpe-U13141    ... ..G. ... ..C. ... ..C. ... ..C. ... ..C. ... ..C. ... ..T. ... ..C.

                380
TMMC-C75      GCA TTT
USNM504259    ... ..C.
USNM504260    ... ..C.
USNM504853    ... ..C.
LAM088901     ... ..C.
MheSAM16387  ... ..C.
Mpe-U13141    ... ..C.

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Figure 4. Aligned sequences for *Mesoplodon perrini* over 384 bp of mitochondrial DNA cytochrome *b*. Identity to reference sequence, TMMC-C75, indicated by dots. Two variable sites, defining three unique haplotypes, were found among the five specimens of *M. perrini*. Sequences from *M. bectori* MheSAM16387 (underlined) and *M. peruvianus* Mpe-U13141 are included for comparison. Position 1 of alignment corresponds to position 14613 of fin whale mtDNA genome (Arnason *et al.* 1991). Diag-

narrows upwards, and the upper part of the skull is triangular in frontal view. In *M. hectori*, the synvertex is flatter, giving the upper part of the skull a rounded box-like shape. In *M. perrini*, the maxillaries below and behind the synvertex on each side of the neurocranium are steep-sided and not greatly inflated, whereas in *M. hectori*, the neurocranium is inflated and the maxillaries are prominent in frontal view on each side of the synvertex. Also, in *M. perrini* the margins of the posteromedial portion of the maxillaries at the uppermost level are sharply angled laterally on each side (90° from the longitudinal median line on the right side, and 110° on the left). In *M. hectori*, these angles are usually gentle (130° – 140°) although one specimen of *M. hectori* from South Africa (PEM 1511/15; Ross 1970) was found to have right side maxillary with a 90° angle. Therefore, this feature may not be a reliable distinguishing character for *M. perrini*.

Associated with the synvertex is the space between the right and left nasals. This is narrow and reverse V-shaped in *M. perrini*, but wide with parallel sides in *M. hectori*. The width of this space can be expressed as the least distance between the anterior prominences of the synvertex, which in *M. perrini* is 2.1%–6.7% ZW, and in *M. hectori*, 8.3%–18.5%.

The premaxillaries of *M. perrini* are noticeably narrower than *M. hectori*. At the position of the antorbital notches, the width of *M. perrini* is 34.5%–35.4% (relative to the distance between the apices of the antorbital notches) compared to 43.3%–53.3% for *M. hectori*. At the position of the superior nares, the width of *M. perrini* is 35.2%–37.2% (relative to ZW) compared to 46.0%–49.0% for *M. hectori*.

There are a number of other, readily visible but less quantifiable features which separate the skulls of these two species, the most significant of which are:

(1) In adult males, the mesorostral groove is fully ossified in *M. perrini*, but unossified in *M. hectori* (unusual in *Mesoplodon*, but the largest mature crania (695 mm and 677 mm CBL) of both sexes of *M. hectori* show little ossification).

(2) *M. perrini* has a basirostral groove extending anterior to the maxillary prominences, while in *M. hectori* this groove is very short in adults and does not extend forward of the prominences.

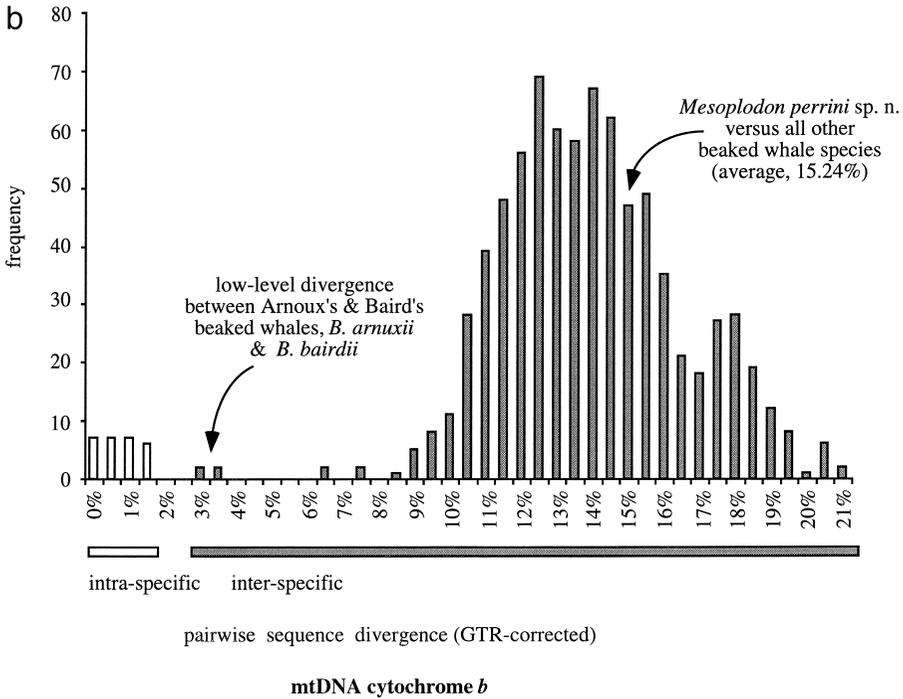
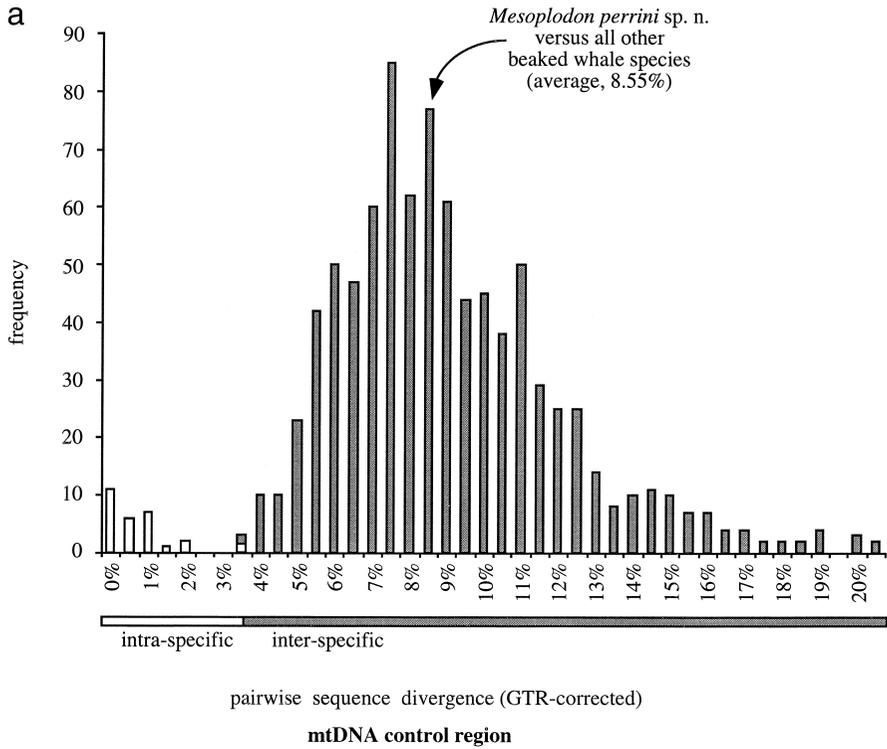
(3) In *M. perrini*, the antorbital notch is formed by the maxillary overlaying the jugal, and the antorbital prominence is formed by the maxillary; in *M. hectori* the antorbital notch is formed by the jugal, and the antorbital prominence is formed by the lacrimal.

(4) Moderately formed maxillary crests are present above the orbit in *M. perrini*, but not in *M. hectori*.

(5) In lateral view, the rostrum of *M. perrini* is deep through to mid-length

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nostic nucleotide position distinguishing *M. perrini* from all 20 previously described species of beaked whales at this locus highlighted in gray.



and thereafter tapers to the tip. In *M. hectori*, the outline is smoothly concave from the pterygoids to the rostrum tip.

Although Harmer (1924) suggested that the structure of the thin part of the mesethmoid which forms the nasal septum was diagnostic for *M. hectori*, our observations suggest that this is a variable character. No significant differences were found in this feature among the specimens of *M. hectori* and *M. perrini* examined. The presence of a dorsal sinus also varies between individuals, and in both species, the septum rises above the level of the premaxillae in the region of the anterior nares.

PREVIOUS ATTRIBUTIONS TO *MESOPLONDON HECTORI* IN THE LITERATURE

A number of publications, in addition to those already mentioned (Mead 1981, Mead and Baker 1987, Henshaw *et al.* 1997), have erroneously used data from specimens of *M. perrini* to represent *M. hectori*. In Mead (1984), reproductive data from specimens of *M. perrini* was used for *M. hectori*. Mead (1989) presented drawings of the cranium, mandible, and a tooth, as well as photographs of the external appearance of the holotype of *M. perrini* (USNM504853), as *M. hectori*. One of these photographs was used by Baker (1990, 1999). Some of these photographs also appeared in Reeves and Leatherwood (1994). Jefferson *et al.* (1993) included some of the figures presented in Mead (1989). In Mead (1993), information on the stomach morphology of *M. perrini* was used for *M. hectori*. The artist's impression of *M. hectori* in Carwardine (1995) was based on photographs of the holotype of *M. perrini*. Messenger and McQuire (1998) used the mtDNA control region sequence from the calf, USNM504259 (Henshaw *et al.* 1997) to represent *M. hectori* in their phylogenetic analyses. Note that we have asked that this Genbank entry be corrected to reflect the true species identity of this specimen. It is possible that there are further publications that we are not aware of which have also made the mistake of using specimens of *M. perrini* to represent *M. hectori*. As no adult male specimens of *M. hectori* were known until relatively recently, images of the holotype of *M. perrini* have unfortunately been used widely to represent this species.

OTHER CHARACTERISTICS

External Appearance

The overall body shape of *M. perrini* is typical of *Mesoplodon* beaked whales, with a relatively small head, a long thorax and abdomen, a deep peduncle,

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Figure 5. Frequency distribution of pairwise sequence divergence within and between the 20 previously known species of beaked whales, based on: (a) 437 bp alignment of mtDNA control region and (b) 384 bp alignment of mtDNA cytochrome *b*. Two representatives used per species where possible. GTR distance correction used to adjust for multiple substitutions. All intraspecific (open bars) and interspecific distances (shaded bars) are shown.

Table 2. Cranial measurements for *Mesoplodon perrini* in mm. Methods of taking measurements follow Moore (1963) taken on right hand side where possible. No cranial measurements taken for USNM504259, as skull was crushed. Measurements currently not available from TMMC-C75. E, estimated length.

Measurement number	Museum number		
	USNM504853	USNM504260	LAM088901
1	563	594	424
2	511	554	365
3	377	414	263
4	412	446	264
5	446	483	314
6	501	541	371
7	310	334	221
8	262	261	203
9	271	282	208
10	271	276	207
11	191	208	162
12	226	232	178
13	99	97	76
14	46	37	34
15	66	61	51
16	54	43	38
17	25	27	19
18	50	59E	35
19	10	16	19
20	15	23	25
21	8	6	14
22	105	110	88
23	41	40	28
24	96	97	77
25	96	98	73
26	159	160	108
27	103	115	67
28	61	62	45
29	32	36	18
30	31	42	25
31	42	39	32
32	32	29	23
33	48	40	31
34	259	267	186
35	168	185	137
36	74	69	64
37	41	43	38
38	81	88	78
39	311	346	246
40	284	317	216
41	236	259	179
42	416	452	—
43	449	—	—
44	90	—	80

Table 2. Continued.

Measurement number	Museum number		
	USNM 504853	USNM 504260	LAM 088901
45	64	70	54
46	0	205	30
sex/age class	male/adult	female/adult	male/calf

Definitions of cranial measurements (numbers in parentheses refer to Moore 1963): 1 = condylobasal length (1); 2 = tip rostrum to posterior extension maxillary plate (7); 3 = tip rostrum to anterior margin superior nares (8); 4 = tip rostrum to anterior point maxillary crest (9); 5 = tip rostrum to posterior extension premaxilla on lateral tip of right premaxillary crest (11); 6 = tip rostrum to posterior extension temporal fossa (10); 7 = tip rostrum to apices of antorbital notches (2); 8 = breadth skull across orbital centres (19); 9 = breadth skull across postorbital process frontals (17); 10 = breadth skull across zygomatic processes squamosals (18); 11 = least breadth skull across posterior margins temporal fossae (20); 12 = greatest breadth skull across occipitals (25); 13 = greatest span occipital condyles (21); 14 = greatest width of an occipital condyle (22); 15 = greatest length of an occipital condyle (23); 16 = greatest breadth foramen magnum (24); 17 = greatest length of right nasal on vertex (15); 18 = length nasal suture (16); 19 = extension right premaxilla posterior to right nasal on vertex (28); 20 = greatest breadth nasals on vertex (26); 21 = least distance between anterior prominences of the synvertex (27); 22 = greatest span premaxillary crests (29); 23 = greatest transverse width of superior nares (37); 24 = least width premaxillae where narrow opposite superior nares (30); 25 = greatest width premaxillae anterior to position of previous (31); 26 = width rostrum in apices of antorbital notches (33); 27 = width rostrum in apices of prominent notches (34); 28 = least distance between main maxillary foramina (41); 29 = least distance between premaxillary foramina (42); 30 = distance posterior margin of left maxillary foramina to anterior margin maxillary prominence (43); 31 = width rostrum at mid-length of rostrum (35); 32 = width premaxillae at mid-length of rostrum (32); 33 = depth rostrum at mid-length rostrum (36); 34 = height of skull (39); 35 = external cranial height; 36 = greatest length of temporal fossa (13); 37 = width of temporal fossa (40); 38 = length of orbit taken from mid-point of frontals (14); 39 = tip rostrum to posterior extension of maxilla between pterygoids (6); 40 = tip rostrum to anterior extension of pterygoid sinus (12); 41 = tip rostrum to most anterior extension of pterygoids (5); 42 = tip rostrum to posterior margin of pterygoid mid-line (3); 43 = tip rostrum to posterior extension of wing of pterygoid (4); 44 = length of vomer visible at surface of palate (44); 45 = width between pterygoid notches (38); 46 = amount added to rostrum because of breakage (45).

and short tail (Fig. 8a–e). The rostrum is relatively short compared to all other species in the genus, except *M. hectori* and *M. peruvianus*. In calves, the rostrum appears to be shorter and stubbier than in adults. The blowhole is broad and crescent-shaped, with anterior-pointing tips. The melon forms a small bulge, and the mouthline is straight. Throat grooves are present. External measurements are shown in Table 4.

The adult male (USNM504853) was dark gray dorsally grading to white ventrally. The ventral side of the tail flukes was pale gray with converging striations and there was a white patch around the umbilicus. The adult female

Table 3. Mandibular measurements for *Mesoplodon perrini*. Measurements follow methods of Moore (1963), taken on right hand side where possible. No measurements available for USNM504259 as mandible has been lost. Measurements currently not available from TMMC-C75. E, estimated length.

Measurement number	Museum number		
	USNM 504853	USNM 504260	LAM 088901
47	516	486	356
48	387	379	289
49	455	402	314
50	120	108	69
51	97	—	—
52	37E	—	21
53	35	37	25
54	47	—	25
55	109	—	9
56	16	—	19
57	52	64	—
58	47	47	—
59	7	12	—
60	n/a	33	n/a
61	9.9 g ^a	37.0 g ^b	—
sex/age class	male/adult	female/adult	male/calf

^a right tooth, dry weight.

^b right tooth, wet weight.

Definitions of measurements (numbers in parentheses refer to Moore 1963): 47 = mandibular length (1); 48 = length from posterior extension of symphysis to condyles (6); 49 = length posterior margin of alveolus to condyles (7); 50 = greatest length of symphysis (2); 51 = greatest height of mandible at coronoid processes (3); 52 = outside height of mandible at midlength of alveolus (4); 53 = inside height of mandible at midlength of alveolus (5); 54 = length of alveolus (8); 55 = width of alveolus (9); 56 = tip of mandible to alveolus (10); 57 = greatest tooth length (11); 58 = greatest tooth width (12); 59 = greatest tooth breadth (13); 60 = height of crown of tooth; 61 = tooth weight.

(USNM504260) was too decomposed to allow information on color pattern to be collected. Calves (USNM504259, LAM088901 and TMMC-C75) are light to dark gray dorsally and white ventrally (Fig. 8a–d). The lower jaw and throat regions are white. A dark gray region extends from the corner of the mouth and encompasses the eye and the rostrum, forming an extended mask. The flippers are medium to dark gray dorsally and white ventrally. There is a lighter-colored patch on the anterodistal portion. The flukes are dark gray dorsally and medium to light gray ventrally. The ventral surface includes a pattern of white striations that converge posteromedially.

Ontogeny and Reproduction

Both adult specimens (USNM504260, female, and USNM504853, male) were considered physically mature based on the fusion of the thoracic epiphyses

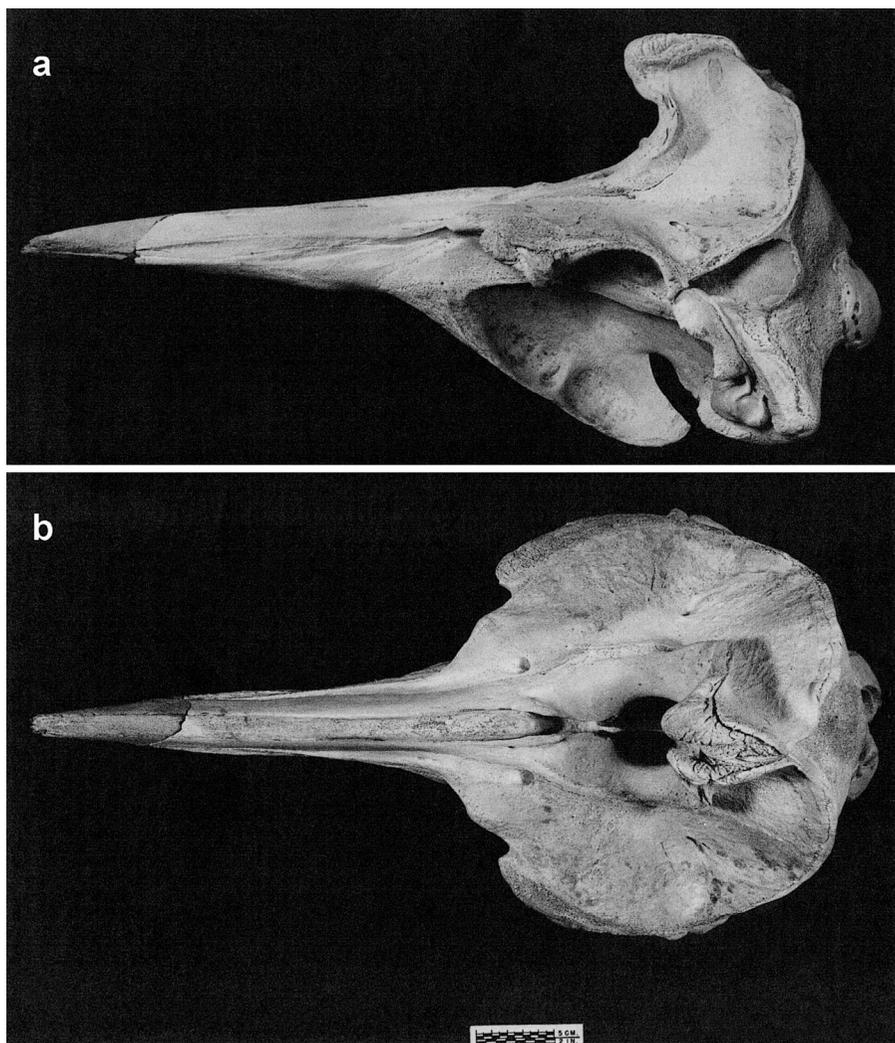
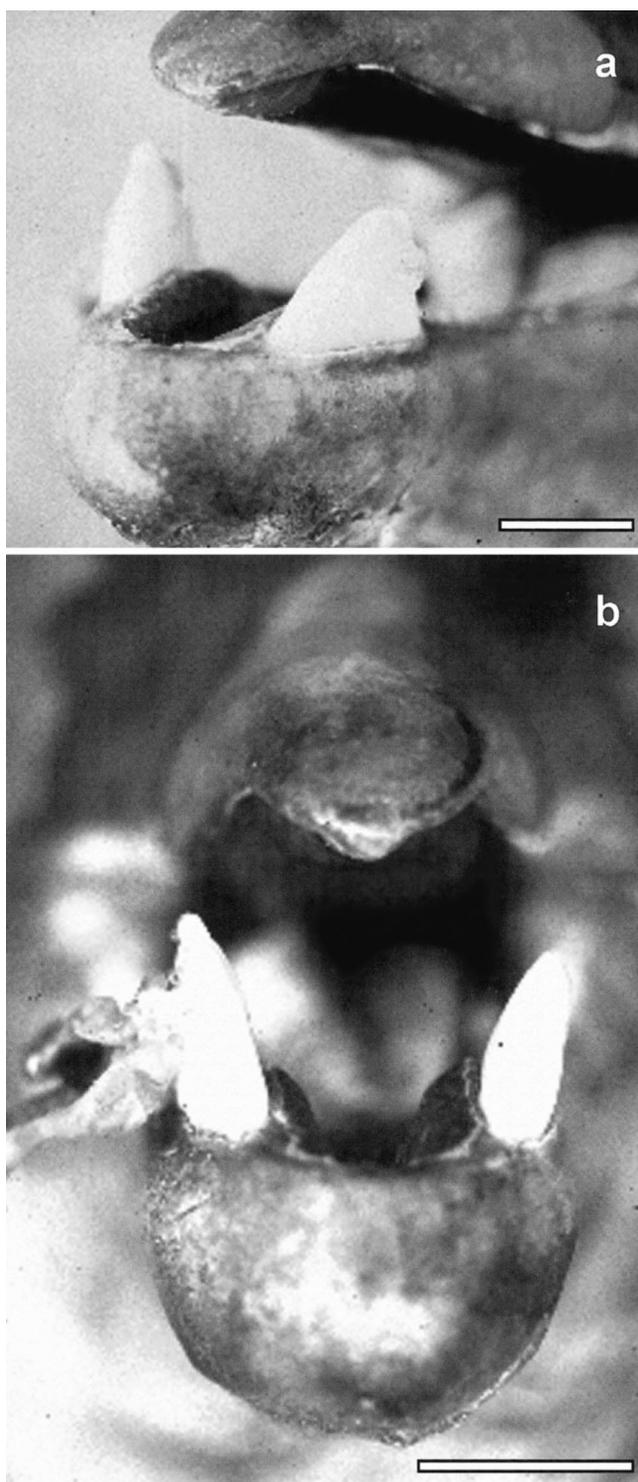


Figure 6. Skull photographs, USNM504853, holotype: (a) lateral view, (b) dorsal view. Scale pattern in (b) = 5 cm, divided into 50-mm squares, and pertains to both figures.

to the centra and the disappearance of the epiphyseal suture (Mead 1981). While the mandibular rami of the male were fused at the symphysis, those of the female were not. The teeth of the male were fully erupted (Fig. 7), and the mesorostral canal completely filled, suggesting that it was sexually mature. The testis weights were; 84.5 g (L), and 115.5 g (R). The adult female appeared to have been dead for about two weeks when discovered (Mead 1981), and was too decomposed for the reproductive organs to be recognizable. It is likely that this animal was the mother of the calf (USNM504259), which had been found in approximately the same location a week earlier (Table 1). Both



animals share the same haplotype at the mtDNA control region and cytochrome *b* (Fig. 3, 4), as expected for a cow-calf pair. Although there has been little opportunity to date for calibration and standardization in the aging of *Mesoplodon* species, thin tooth sections were prepared from the right tooth of both adult specimens, and the cemental growth layer groups (GLG's) counted, giving an approximate age of nine years each, although the male appeared the more mature of the two from cranial features (Mead 1981).

The 245-cm calf (LAM088901) had a squid eye lens in its stomach, which suggests that it had been weaned. There are no data on stomach contents for the other two calves (USNM504259 and TMMC-C75), but the fimbriated edge on the tongue of the former animal suggests that it was still suckling (Fig. 8d). The Monterey calf (TMMC-C75) had small, immature testes, which were elliptical in shape and weighed approximately 1.5 g each.

NATURAL HISTORY

Food Habits

Only two of the animals had stomach contents. The stomach of a third (TMMC-C75) was collected, but is currently not available for examination. A squid eye lens, not identifiable to species, was found in the stomach of the second calf (LAM088901). Two lower beaks of the squid, *Octopoteuthis deletron*, and a fragment of an unidentifiable vertebrate were found in the stomach of the adult female (USNM504260; Mead 1981). We assume that like many other beaked whales, this species mainly eats pelagic squid.

Behavior

The adult male (USNM504853) bore a number of white, linear scars on its postcranial flanks which were probably inflicted by the teeth of other males of the species. However, it is noted that the scars on the adult male appear to have been made with a single tooth, rather than with two teeth simultaneously, as might be expected in species with apical teeth (e.g., Heyning 1984).

Parasites

Three soft-stalked barnacles, *Conchoderma auritum*, were found on the teeth of the adult male (USNM504853), and a number of cysts of the cestode, *Phyllobothrium* sp., were found encased in the blubber. Several oval scars (approximately 3 × 5 cm) were found on the flanks. The Monterey calf (TMMC-C75) bore three similar scars, in various stages of healing. Such scars are likely due to cookie-cutter shark attacks (*Isistius* spp.; Jones 1971). This calf was

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Figure 7. Teeth of adult male (USNM504853) *in situ*: (a) oblique lateral view; (b) anterior view. Scale bars = 30 mm. Photograph credit: J. G. Mead.

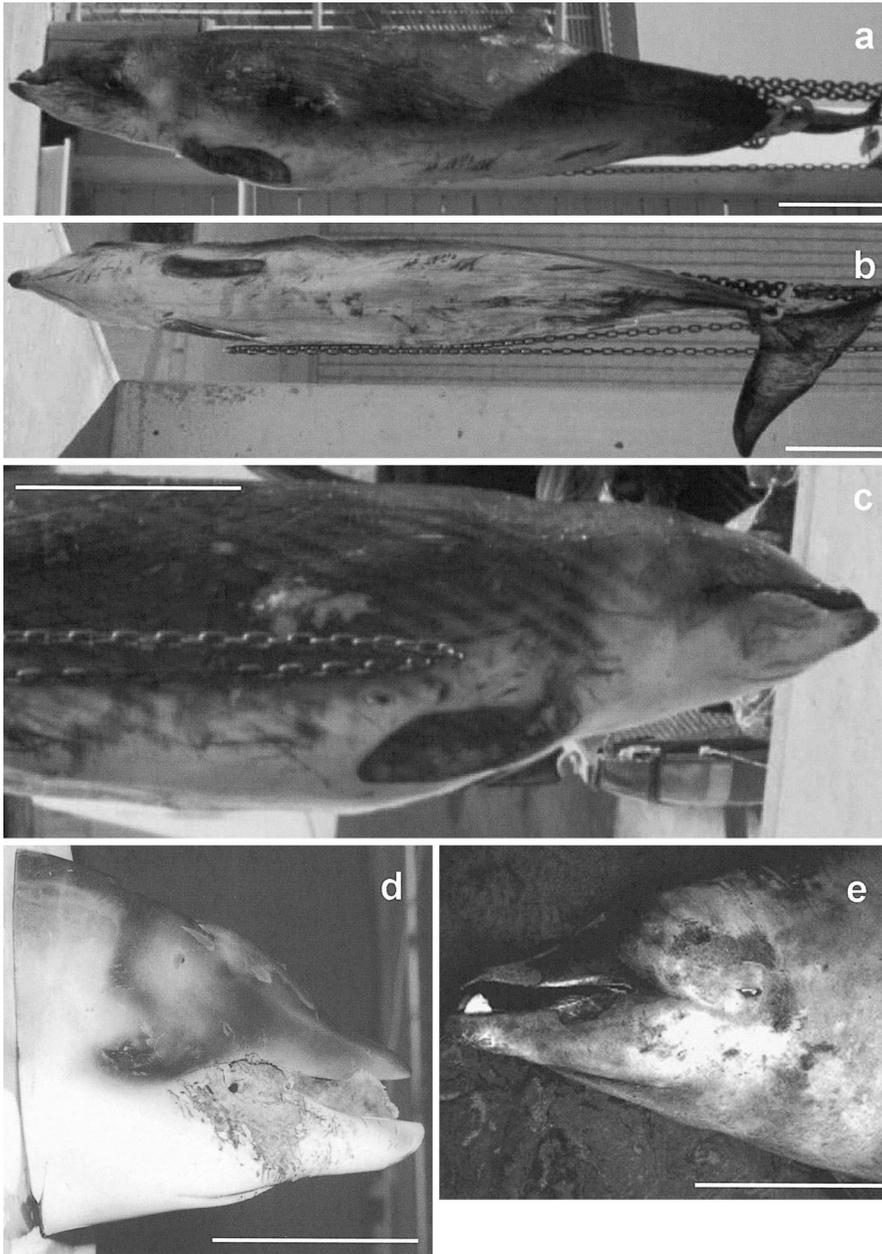


Figure 8. External photographs. (a) left lateral view of calf (TMMC-C75), scale bar = 30 cm; (b) ventral view of calf (TMMC-C75), scale bar = 30 cm; (c) right lateral view of calf (TMMC-C75), scale bar = 30 cm; (d) right lateral view of head of calf (USNM504259), scale bar = 20 cm; (e) left lateral view of head of adult male (USNM504853), scale bar = 24 cm. Note that striped pattern on right lateral side of calf (TMMC-C75) is the imprint caused by bed of utility truck on which animal was lying. Photograph credits: (a–c) M. Haulena; (d, e) G. Carsten and J. G. Mead.

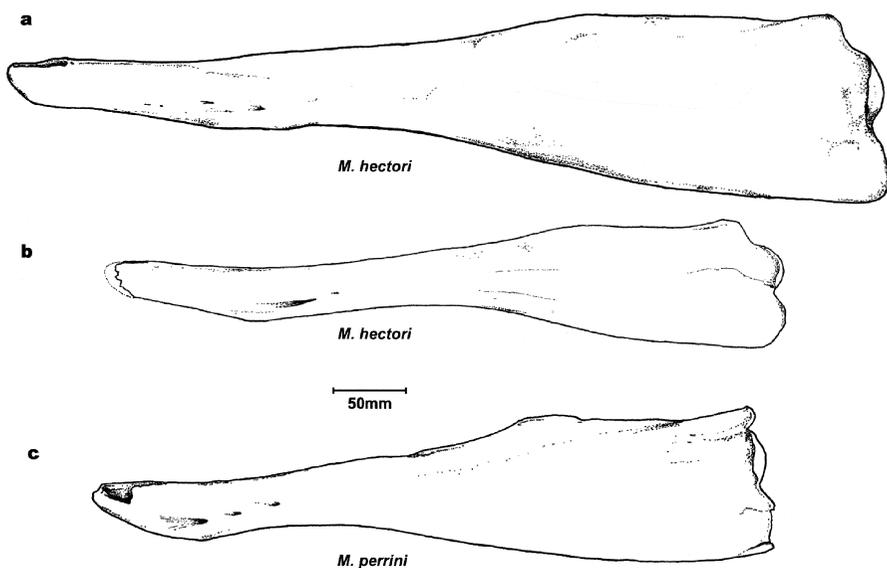


Figure 9. Lateral view of mandibular ramus of *Mesoplodon hectori* (a, NMNZ2173 adult male; b, NMNZ614 juvenile male) and *M. perrini* (c, USNM504853 adult male).

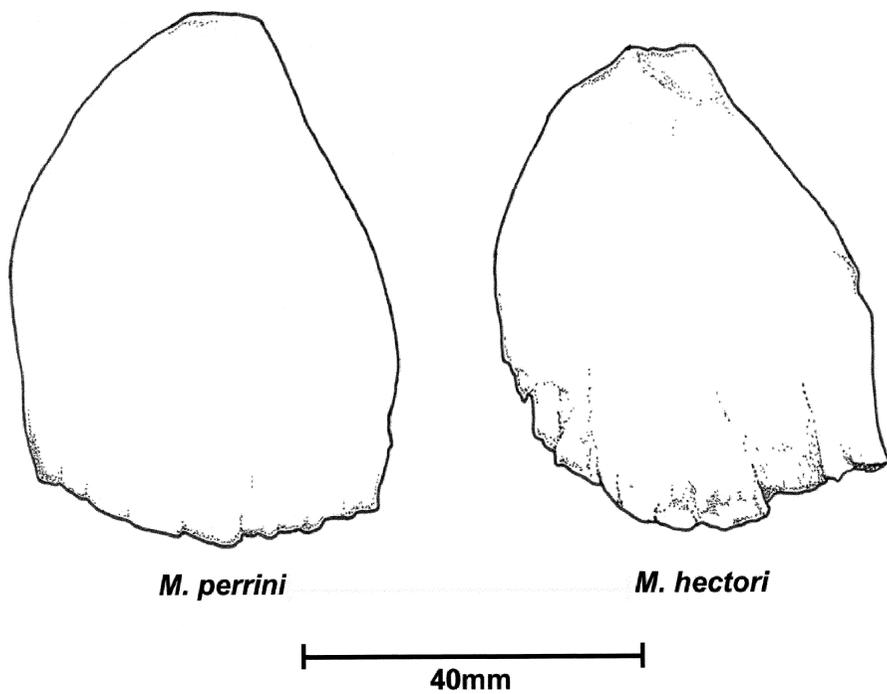


Figure 10. Adult male tooth of *Mesoplodon perrini* (USNM504853) and *M. hectori* (NMNZ2173). Right tooth of each species is shown, with anterior margin facing left.

Table 4. External measurements for *Mesoplodon perrini*. Due to extent of decomposition, few measurements were available from adult female (USNM504260).

Museum or field number:	USNM504853		USNM504260		USNM504259		LAM088901		TMMC-C75	
	Male/adult	%	Female/adult	%	Male/calf	%	Male/calf	%	Male/calf	%
Sex/age class:	cm	%	cm	%	cm	%	cm	%	cm	%
Measurement:	cm	%	cm	%	cm	%	cm	%	cm	%
Total length	390.0	100.0	443.0	100.0	210.0	100.0	245.0	100.0	223.5	100.0
Snout to center of blowhole	35.1	9.0	—	—	22.7	10.8	27.0	11.0	18.5	8.3
Snout to center of eye	42.5	10.9	—	—	25.3	12.0	28.5	11.6	25.5	11.4
Snout to angle of mouth	24.0	6.2	—	—	19.5	9.3	15.2	6.2	14.0	6.3
Snout to ear	50.2	12.9	—	—	29.6	14.1	33.7	13.8	—	—
Snout to anterior insertion of flipper	72.0	18.5	—	—	48.4	23.0	51.7	21.1	47.0	21.0
Snout to center of umbilicus	150.0	38.5	—	—	—	—	123.4	50.4	105.5	47.2
Snout to genital slit (center)	254.0	65.1	—	—	140.0	66.7	162.0	66.1	142.0	63.5
Snout to anus	285.0	73.1	—	—	159.0	75.7	184.8	75.4	160.1	71.6
Snout to tip of dorsal fin	240.0	61.5	274.0	61.9	140.0	66.7	162.9	66.5	146.0	65.3
Girth at eye	120.0	30.8	—	—	—	—	84.5	34.5	72.5	32.4
Girth at axilla	196.0	50.3	—	—	—	—	127.0	51.8	107.0	47.9
Maximum girth	230.0	59.0	—	—	—	—	—	—	119.5	53.5
Girth at anus	130.0	33.3	—	—	—	—	90.0	36.7	70.0	31.3
Girth midway anus to fluke notch	66.0	16.9	—	—	—	—	—	—	48.0	21.5
Height at same place as above	30.6	7.8	—	—	—	—	—	—	24.0	10.7
Thickness at same place as above	9.0	2.3	—	—	—	—	—	—	9.5	4.3
Projection lower/upper jaw	1.6	0.4	—	—	0.6	0.3	0.6	0.2	2.0	0.9
Length of eye opening	3.2	0.8	—	—	—	—	—	—	4.0	1.8
Center of eye to ear	9.0	2.3	—	—	5.4	2.6	7.0	2.9	—	—
Center of eye to angle of mouth	18.8	4.8	—	—	6.0	2.9	17.1	7.0	12.5	5.6
Blowhole width	9.9	2.5	—	—	4.8	2.3	5.8	2.4	5.7	2.6
Length of throat grooves	20.0	5.1	—	—	9.7	4.6	19.7	8.0	14.0	6.3

Table 4. Continued.

Museum or field number:	USNM504853		USNM504260		USNM504259		LAM088901		TMMC-C75	
	Sex/age class:	Male/adult	Female/adult	Male/adult						
Measurement:	cm	%	cm	%	cm	%	cm	%	cm	%
Flipper length, anterior	46.0	11.8	40.0	9.0	28.0	13.3	31.5	12.9	30.5	13.6
Flipper length, posterior	29.0	7.4	32.0	7.2	19.0	9.0	20.1	8.2	24.0	10.7
Flipper width, maximum	13.2	3.4	—	—	7.6	3.6	9.0	3.7	8.5	3.8
Fluke width	103.0	26.4	89.0	20.1	46.7	22.2	52.0	21.2	58.0	26.0
Fluke depth	32.0	8.2	—	—	18.0	8.6	20.8	8.5	19.0	8.5
Depth of fluke notch	NA	—	—	—	1.9	0.9	NA	—	1.2	0.5
Dorsal fin height	19.0	4.9	—	—	10.2	4.9	13.6	5.6	9.0	4.0
Length dorsal fin base	50.0	12.8	—	—	23.0	11.0	—	—	18.0	8.1

severely emaciated, with minimal body fat and atrophied muscles. No parasites were found in gross necropsy, but a histological examination of abscesses in the periumbilical region revealed that they contained degenerating cestodes (likely *Phyllobothrium* spp., possibly *Phyllobothrium delphini*) and other foreign material. Structures resembling parasitic granulomas were found within the gastrointestinal tract and one of the lymph nodes (necropsy performed by F. Gulland, University of California at Davis; details courtesy of M. Haulena).

Distribution

This species is known from five specimens found beachcast along the Californian coast between Torrey Pines State Reserve, just north of San Diego (32°55'N, 117°15'W) and Fisherman's Wharf, Monterey (36°37'N, 121°55'W). Although this stranding pattern is suggestive of an eastern North Pacific distribution, there are too few records to date to draw any bounds on this. Little can be concluded from the presence of cookie-cutter shark scars on the Monterey calf. *Isistius* spp. are limited in their northern distribution, at least in surface waters (Nakano and Tabuchi 1990), but the occurrence of such scars on cetaceans is not (Jones 1971). This suggests either that these cetaceans are migratory and pass through the territory of *Isistius* spp., or that the distribution of *Isistius* spp. extends farther north in deeper waters and they attack cetaceans when they dive. Given the habitat preferences of other ziphiids, we assume that *M. perrini* is found primarily in oceanic waters, over 1,000 m in depth.

DISCUSSION

According to the International Code of Zoological Nomenclature (ICZN), formal classification of *M. perrini* ideally requires genetic validation of the holotype of *M. bectori*, as four of the five known specimens of *M. perrini* were described previously as this species (Mead 1981). The holotype of *M. bectori* is held by the British Museum (BM(NH) 1677/76.2.16.3), and consists of the skull, mandible, scapulae, hyoids, cervical vertebrae and flippers of a juvenile male collected in Titahi Bay, Wellington, New Zealand, in the 19th century (Flower 1878; Gray 1871). We have attempted, but not been successful in extracting and amplifying native DNA from the *M. bectori* holotype. This may be due to the coat of varnish on this specimen, the acidic components of which can degrade the already low levels of endogenous DNA contained in skeletal material (Cooper 1994). In the absence of genetic data from the holotype of *M. bectori*, validated specimens from New Zealand and Australia have been used to represent this *M. bectori* in these analyses.

Given the increasing use of genetic information as a universal character in species identification, systematics, and biodiversity assessment (Bisby 2000, Wilson 2000), the designation of genetic voucher material should be considered for all taxa. It has been suggested that mtDNA typing of holotype specimens should become part of standard museum protocol (Dalebout 2002), but

it is recognised both that: (1) not all specimens will retain sufficient native DNA for analysis due to a combination of age, the nature of the material available (*e.g.*, bone, tooth, pelts, feathers), and museum preparation and storage methods and (2) not all specimens will be amenable to current DNA extraction techniques (*e.g.*, Wayne *et al.* 1999). In such cases, genetic material should be obtained from other validated specimens of the species in question (*e.g.*, Dizon *et al.* 2000). Genetic voucher material, in the form of DNA sequences from a suite of loci, could be archived both at the institution holding the holotype (or alternative validated specimen from which these data were derived), as well as in the international genetic database, Genbank. When describing new species, a genetic description should also be included wherever possible.

A recent analysis of discovery trends has suggested that at least 40 species of large marine animals still remain to be described (Paxton 1998). If so, it is likely that several new cetacean species will be among them, including at least one new form of Bryde's whale, *Balaenoptera edeni* sp. (*e.g.*, Baker *et al.* 1996, Yoshida and Kato 1999), and possibly further species of ziphiids. The current discovery represents the second new species of *Mesoplodon* discovered in the last decade. Both were dependent on the opportunistic collection of beachcast specimens and victims of fisheries bycatch (Reyes *et al.* 1991, this paper). Yet, there is no reason to assume that all cetacean species can be encountered in this way. Some may be distributed in areas far from shore or shore-bound currents, where human presence is still minimal. To ensure that such species do not go undocumented, we recommend that biopsy samples be collected wherever possible from animals encountered on sighting cruises. In addition to traditional morphological information, the collection of tissue samples from stranded and incidentally caught animals should also become standard procedure.

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