

RESURRECTION OF *MESOPLODON TRAVERSII*
(GRAY, 1874), SENIOR SYNONYM OF
M. BAHAMONDI REYES, VAN WAEREBEEK,
CÁRDENAS AND YÁÑEZ, 1995
(CETACEA: ZIPHIIDAE)

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ABSTRACT

Mesoplodon traversii (Gray, 1874) is shown to be a senior synonym of the recently described beaked whale *Mesoplodon bahamondi* Reyes *et al.*, 1995 on the basis of a phylogenetic analysis of mitochondrial DNA control region sequences. The mandible and teeth of *M. traversii*, first reported in 1873 by Hector as *Dolichodon layardii*, are redescribed. The species can be distin-

guished by features of the calvaria; including the large jugal, broad rostrum, and small distance between premaxillary foramina. The male teeth, which are large and spade-shaped with a strong terminal denticle, are also diagnostic. *M. traversii* is known only from Pitt Island and White Island, New Zealand and Robinson Crusoe Island, Juan Fernandez Archipelago, Chile.

Key words: beaked whales, *Mesoplodon*, taxonomy, morphology, phylogenetics, mtDNA, South Pacific.

In 1873 James Hector, then director of the Colonial Museum in New Zealand (now Museum of New Zealand Te Papa Tongarewa), reported and illustrated the partially damaged mandible and teeth of a beaked whale collected in 1872 from Pitt Island, Chatham Islands, New Zealand. He assigned these to the species "*Dolichodon layardii* Scamperdown Whale" described by J. E. Gray from South Africa in 1865. In 1874 Gray concluded that the specimen from Pitt Island represented a new species, for which he proposed the name *Dolichodon traversii*, noting that "*Mesoplodon layardi* (or as I should call it, *Dolichodon layardi*) has a much longer and attenuated lower jaw, and much more slender teeth than the Chatham Island specimen." Hector (1878), however, regarded *Dolichodon traversii* as synonymous with *Mesoplodon layardi* [sic]. McCann (1962) agreed with Hector and illustrated the tooth of this specimen as representing *M. layardii*, the now generally accepted scientific name for the strap-toothed whale. Hector's original specimen is extant, in the condition in which it was collected in 1872, in the marine mammal collections of the Museum of New Zealand Te Papa Tongarewa in Wellington, New Zealand, as NMNZ 546 (Fig. 1).

A second specimen of interest lay unexamined for many decades in the MacGregor Collection of the University of Auckland. This specimen, a beaked whale calvaria from White Island, New Zealand, was collected in the 1950s and was recently described on morphological grounds as *Mesoplodon ginkgodens* by Baker and van Helden (1999). However, subsequent phylogenetic analyses of DNA sequences from the White Island specimen by Dalebout indicated that it did not represent this species, or any other *Mesoplodon* for which DNA sequences were then available. Concurrently, two other authors (JCR and KVV) recognized the White Island specimen as being *Mesoplodon babamondi* after comparing the published photographs and description in Baker and van Helden (1999) with the holotype of *M. babamondi* Reyes, Van Waerebeek, Cárdenas and Yáñez, 1995. *M. babamondi* is also known only from a damaged calvaria, found on Robinson Crusoe Island, Juan Fernández Archipelago, Chile, in 1986. Although the Robinson Crusoe Island specimen was without mandible and teeth, features of which are usually diagnostic for species of the genus *Mesoplodon*, there were sufficient differences in the specimen's morphology to warrant its description as a new species (Reyes *et al.* 1995). Subsequently, Baker (2001) re-examined the White Island specimen and concluded that it was conspecific with *M. babamondi*. Meanwhile, a sample of mtDNA was obtained from the holotype of *M. babamondi*, and resulting sequences were

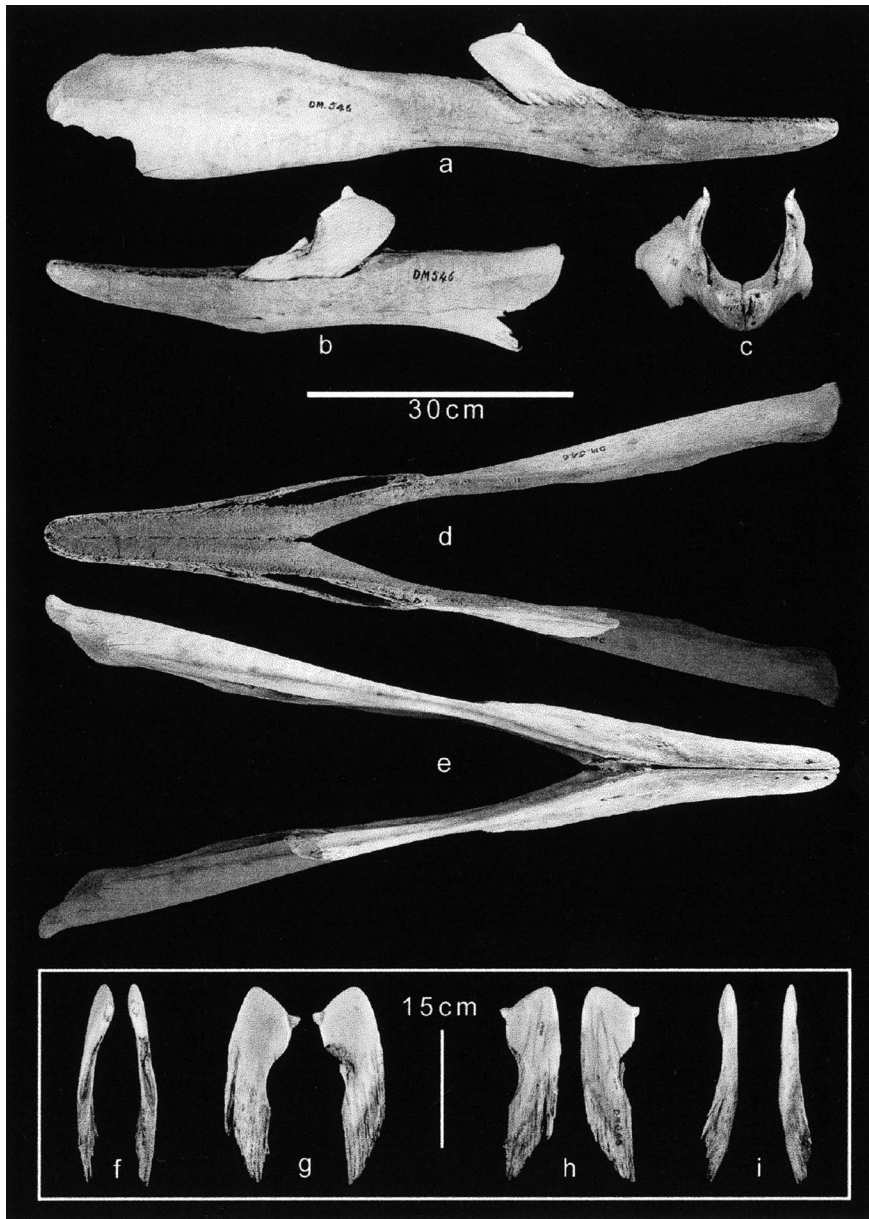


Figure 1. Mandible and teeth of *Mesoplodon traversii*, Holotype NMNZ 546: (a) right ramus with tooth *in situ*, (b) left ramus with tooth *in situ*, (c) anterior view of mandible with teeth *in situ*, (d) dorsal view of mandible (with posterior portion of right side reflected on to left side as ghost image to give idea of complete mandible), (e) ventral view of mandible (with ghosted reflection as in [d]), (f) anterior view of teeth, (g) external view of teeth, (h) internal view of teeth, (i) posterior view of teeth.

found to align closely with those from both the White Island and Pitt Island specimens.

Here, we present details of molecular and morphological evidence unifying these three specimens (from Pitt Island, White Island, and Robinson Crusoe Island), resulting in the synonymy of *M. bahamondi* with *M. traversii*. The molecular evidence for this conclusion is based on phylogenetic analyses using a validated DNA reference database of mitochondrial (mt) DNA sequences.¹ This database, which is housed at the University of Auckland, consists of reference sequences from all known beaked whale species, including some not available in previous studies (Dalebout *et al.* 1998, Henshaw *et al.* 1997). We also confirm the morphological distinctiveness of *Mesoplodon traversii*, based on studies of the combined calvariae, mandible, and teeth of the three known specimens.

METHODS

Material Examined

1. Mandible and two teeth (NMNZ 546) held in Museum of New Zealand Te Papa Tongarewa (and genetic sample of 431 base pairs (bp) of the mtDNA control region from dentine-cementum powder from one of the teeth). Collected in 1872 by H. H. Travers, from Pitt Island, Chatham Islands (44°17'S, 176°15'W), New Zealand. Holotype of *Mesoplodon traversii*. This is the specimen reported by Hector (1873) and named by Gray (1874) and is the first material known of this species.

2. Calvaria (and genetic sample of 295 bp of the mtDNA control region from bone powder from the rostral portion of the premaxilla) held in Auckland University School of Biological Sciences, MacGregor Collection (no reference number available), collected in 1950s (exact date unknown) from White Island (35°31'S, 177°11'E), New Zealand.

3. Calvaria (and genetic sample of 236 bp of the mtDNA control region from bone powder from the occipital condyle) of *Mesoplodon bahamondi* type specimen (MNHNC 1156), held in Museo Nacional de Historia Natural de Chile and collected in 1986 from Robinson Crusoe Island (33°37'S, 78°53'W), Juan Fernández Archipelago, Chile.

DNA Extraction and PCR Amplification from Museum Specimens

DNA was extracted from a range of *Mesoplodon* teeth in the NMNZ collections using methods described in Pichler *et al.* (2001). Using the Polymerase Chain Reaction (PCR), a 437 bp fragment of the mtDNA control region (D-loop) was amplified from the Pitt Island specimen using the primers M13-Dlp1.5-L and Dlp5-H.¹ PCR amplification followed standard protocols (Pal-

¹ Dalebout, M. L. Species identity, genetic diversity and molecular systematic relationships among the Ziphiidae (beaked whales). PhD thesis, School of Biological Sciences, University of Auckland, Auckland, New Zealand (submitted for examination October 2001).

umbi 1996, Saiki *et al.* 1988), except for the addition of bovine serum albumin (BSA) solution (0.5–1 mg/ml) to help overcome the effect of the inhibiting substances that often accumulate in archaeological material (Pääbo 1990). PCR products were sequenced in both directions on an ABI 377 automated DNA sequencer (Applied Biosystems Inc.) using BigDyeTM Dye Terminator Chemistry.

The resulting sequence (431 bp) was aligned by eye to the reference sequences in the beaked whale DNA database, which includes representatives of *M. layardii*. All specimens in this database are validated by diagnostic skeletal material and/or photographic records, held in museums and archives.¹ With the recent addition of a mtDNA control region sequence (236 bp) from the holotype of *M. bahamondi* (*i.e.*, the Robinson Crusoe Island specimen), this database now includes representatives of all 21 known beaked whales (Dalebout *et al.* 2002). The mtDNA sequence data from the White Island specimen (295 bp) were also included in these analyses. Only the first 301 bp of the full length 437 bp reference sequence alignment was used for subsequent phylogenetic analyses due to the shorter sequences obtained from the *M. bahamondi* holotype and the White Island specimen. The aligned sequence file and further information on PCR primers are available from the University of Auckland's Ecology and Evolution Research Group, and can be found on their website.²

Phylogenetic Analyses

Phylogenetic relationships among these specimens and representatives of all other known beaked whale species were reconstructed from the mtDNA control region sequence data using distance-based (neighbor-joining) and parsimony methods as described by Dalebout.¹ For neighbor-joining analyses, general time-reversible (GTR) distances were used to correct for multiple substitutions. For parsimony analyses, the heuristic search option (20 replicates, random sequence addition) with tree bisection-reconnection was used. Baird's beaked whale *Berardius bairdii*, which likely represents the basal genus in this family (*e.g.*, Dalebout *et al.* 1998), was used as an outgroup. All analyses were performed using the program PAUP* 4.0 beta 8 (Swofford 1999).

RESULTS

Molecular Genetic Identification and Distinctiveness

Phylogenetic analyses of mtDNA control region sequences (301 bp consensus alignment) strongly grouped the holotype of *M. bahamondi* (MNHNC 1156) and the White Island specimen with the holotype of *M. traversii* (NMNZ 546; bootstrap score, 100%) indicating that all three specimens are the same species, distinct from *M. layardii* and all other species of beaked whale (Fig. 2). All species-specific groupings received high bootstrap scores

² <http://www.dna-surveillance.auckland.ac.nz>

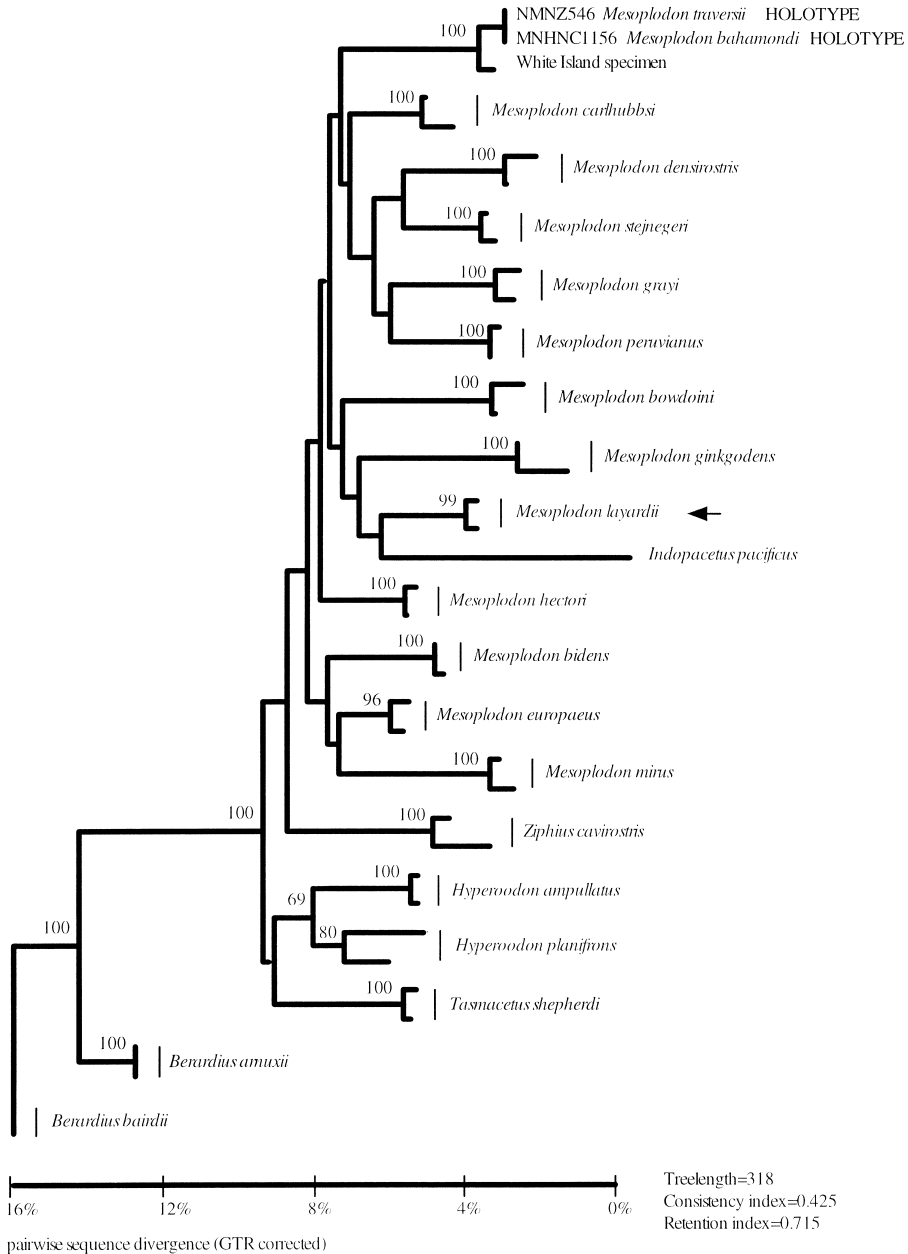


Figure 2. Phylogenetic relationships among all 20 previously described beaked whale species (excluding *M. perrini* sp. n., Dalebout *et al.* 2002) based on neighbor-joining analysis of mtDNA control region sequences (301 bp consensus length alignment). Numbers above internal nodes indicate bootstrap values $\geq 50\%$. All species represented by two reference specimens where possible. Results from parsimony analyses were in agreement with neighbor-joining tree at all nodes relevant to this paper. White box highlights grouping of holotype of *Mesoplodon traversii* (NMNZ 546), with holotype of *M. bahamondi* (MNHNC 1156), and White Island specimen, to exclusion of all other beaked whale species. Arrow highlights position of *M. layardii*, the species with which NMNZ 546 was previously synonymized. 'Sequences for *M. peruvianus* (MpeJCR1926) submitted to Genbank (Accession No.'s AF492413-AF492414).'

($\geq 80\%$) in these analyses, although higher-level relationships were generally not well resolved (*i.e.*, bootstrap scores $\leq 50\%$). Only the neighbor-joining tree is shown. This tree did not differ significantly from the parsimony tree at nodes relevant to this paper. The sequences obtained from NMNZ 546, MNHNC 1156, and the White Island specimen have been deposited in Genbank (Accession No.'s AF439992–AF439994).

Over the 236 bp mtDNA control region segment covered by sequence data from all three specimens, the *M. traversii* holotype shares the same haplotype as the *M. bahamondi* holotype, and differs from the White Island specimen by three transition substitutions (1.35%; Fig. 3.) The *M. traversii* holotype differs from *M. layardii* by 9.66% over this same fragment. Previous comparisons of intra- and interspecific pairwise sequence divergence among beaked whales have suggested that intraspecific variation is less than 2%, while interspecific variation is greater than 4% in this group (Dalebout *et al.* 1998).

Synonymy

The Pitt Island specimen has now been shown by phylogenetic analyses to be distinct from *M. layardii*, but conspecific with the holotype of *M. bahamondi* and the White Island calvaria. By chronological priority, the species represented by these three specimens must therefore take the name *Mesoplodon traversii* (Gray, 1874).

Mesoplodon traversii (Gray, 1874)

Dolichodon layardii; Hector, 1873: 166, pl. III, fig. 1–5 [not *Ziphius layardii* Gray, 1865].

Dolichodon traversii Gray, 1874: 96.

Mesoplodon layardi [sic]; Hector, 1878: 341 [not *Ziphius layardii* Gray, 1865].

Mesoplodon layardi [sic]; McCann, 1962: pl.2, fig. 5a [not *Ziphius layardii* Gray, 1865].

Mesoplodon layardi [sic]; Hershkovitz, 1966: 134 [not *Ziphius layardii* Gray, 1865].

Mesoplodon bahamondi Reyes, Van Waerebeek, Cárdenas and Yañez, 1995: 32, fig. 1A–F, 2A. **New synonymy**

Mesoplodon ginkgodens; Baker and van Helden, 1999: 239, fig. 2,4 [not *Mesoplodon ginkgodens* Nishiwaki and Kamiya, 1958]

Mesoplodon bahamondi; Baker, 2001

Morphological Description

Measurements, figures, and a full description of the calvaria of *M. traversii* from Chile can be found in Reyes *et al.* (1995) (as *M. bahamondi*) and from White Island in Baker and van Helden (1999) (as *M. ginkgodens*). For sake of completeness, reformatted photographs of the White Island calvaria are presented here (Fig. 4) to accompany the new illustrations of the mandible and teeth of the *M. traversii* holotype (Fig 1).

The main distinguishing features of the calvaria of *M. traversii* have been

	10	20	30	40	50	60	70
<i>M. traversii</i> MNMZ546	G-AAAAGTCT	TATTGTAGAA	TCACCATAAC	CCTACAGTAC	TACGTCAGTA	TTGAAAAA-A	AAAATCTCAC
<i>M. traversii</i> WhiteIsland
<i>M. traversii</i> MNHNC1156	??????????	??????????	??????????	??????????	??????????	??????????
<i>M. layardii</i> MlaySAM18078	.A.....	.C.A..C..T.....	.A.....	.T..C..
<i>M. bowdoini</i> MbowNMNZ619	.A.....TC.....	.T.....	.G.....	.T..CT..
<i>B. bairdii</i> BbaSW4965	.A.....	.CT.....	.G..A.....	.C.....	.G.....CT.....
<i>M. traversii</i> MNMZ546	AGTACATTTA	CTGFATTAA	CACACATACC	CATCCACTCA	TACGCT-AAT	AT-ATGGTCT	CT-CTTCAGG
<i>M. traversii</i> WhiteIslandG.....	C.....A.....
<i>M. traversii</i> MNHNC1156
<i>M. layardii</i> MlaySAM18078T..AG.A	.CT..C.G	.G.AT..A.CG..
<i>M. bowdoini</i> MbowNMNZ619A..A..	.TC..T.C.	C.TA..A.CG..
<i>B. bairdii</i> BbaSW4965	.AC.....G.....C.TA	TTAAT..C.	CC.A.CA..
<i>M. traversii</i> MNMZ546	ACTGTATGTA	TATATATACT	ATGTATAACT	GTGCATTGAT	TTATTTTTCAC	TACGGAGAGT	TAAAGCTCGT
<i>M. traversii</i> WhiteIsland
<i>M. traversii</i> MNHNC1156
<i>M. layardii</i> MlaySAM18078	.G.....	G.....
<i>M. bowdoini</i> MbowNMNZ619	.G.....
<i>B. bairdii</i> BbaSW4965
<i>M. traversii</i> MNMZ546	AATTAATTTT	TTTTATTTTA	CATAAGTACA	TAATTGTCAT	TATT-ATACA	TGTGCCCGGT	CCATTAGATC
<i>M. traversii</i> WhiteIsland
<i>M. traversii</i> MNHNC1156
<i>M. layardii</i> MlaySAM18078A.CG..
<i>M. bowdoini</i> MbowNMNZ619C.....	G.....	C.....	T.....
<i>B. bairdii</i> BbaSW4965A.....GA.TG..
<i>M. traversii</i> MNMZ546	ACGAGCTTAA	TTACCATGCC	CGCTGAAACC	AGCAACCGT	TTGGCAGGGA	TCCCTCTCT	CGCACGGGSC
<i>M. traversii</i> WhiteIsland	??????????	??????????	??????????	??????????	??????????
<i>M. traversii</i> MNHNC1156	??????????	??????????	??????????	??????????	??????????
<i>M. layardii</i> MlaySAM18078C.....C.....
<i>M. bowdoini</i> MbowNMNZ619C.....C.....
<i>B. bairdii</i> BbaSW4965C.....C.....
<i>M. traversii</i> MNMZ546	CCATCCATCG	TGGGGGTAGC	TAATCTTGCC	TTTTATAAGA	CATCTGGTTC	TTACTTCAGG	ACCAITTTAA
<i>M. traversii</i> WhiteIsland	??????????	??????????	??????????	??????????	??????????	??????????	??????????
<i>M. traversii</i> MNHNC1156	??????????	??????????	??????????	??????????	??????????	??????????	??????????
<i>M. layardii</i> MlaySAM18078
<i>M. bowdoini</i> MbowNMNZ619
<i>B. bairdii</i> BbaSW4965G.....A.....	G.....
<i>M. traversii</i> MNMZ546	CTTAAATCG	CCCACCTC
<i>M. traversii</i> WhiteIsland	??????????	??????????
<i>M. traversii</i> MNHNC1156	??????????	??????????
<i>M. layardii</i> MlaySAM18078
<i>M. bowdoini</i> MbowNMNZ619
<i>B. bairdii</i> BbaSW4965

Figure 3. Aligned mitochondrial DNA control region sequences for *Mesoplodon traversii* as based on reference database alignment (consensus length, 437 bp) including all known beaked whale species (see footnote 1). Identity to the top sequence MNMZ 546 is indicated by dots. Dashes indicate insertion-deletion (indel) events. Note that some indels pertain to beaked whale species not included in this figure, but have been retained to preserve alignment. Sequences representing morphologically similar strap-toothed whale *M. layardii* (tooth form) and Andrew's beaked whale *M. bowdoini* (cranial features; Reyes *et al.* 1995) are included to show their genetic distinctiveness. Baird's beaked whale *Berardius bairdii* included as an outgroup. Position 1 of this alignment corresponds to position 15891 of the fin whale *Balaenoptera physalus* mtDNA genome (Arnason *et al.* 1991).

summarized by Reyes *et al.* (1995) and Baker (2001) as follows (see also Fig. 1, 4):

1. Presence of a large jugal, comprising most of the antorbital process and exposed laterally. The lacrimal does not extend sufficiently anteriorly to be part of the antorbital tubercle, and the length of its outer margin is contained approximately four times in the length of the outer margin of the jugal.

2. The relative width of the rostrum at its base, between the apices of the antorbital notches is greater than in other mesoplodonts: 66.9% of the zy-

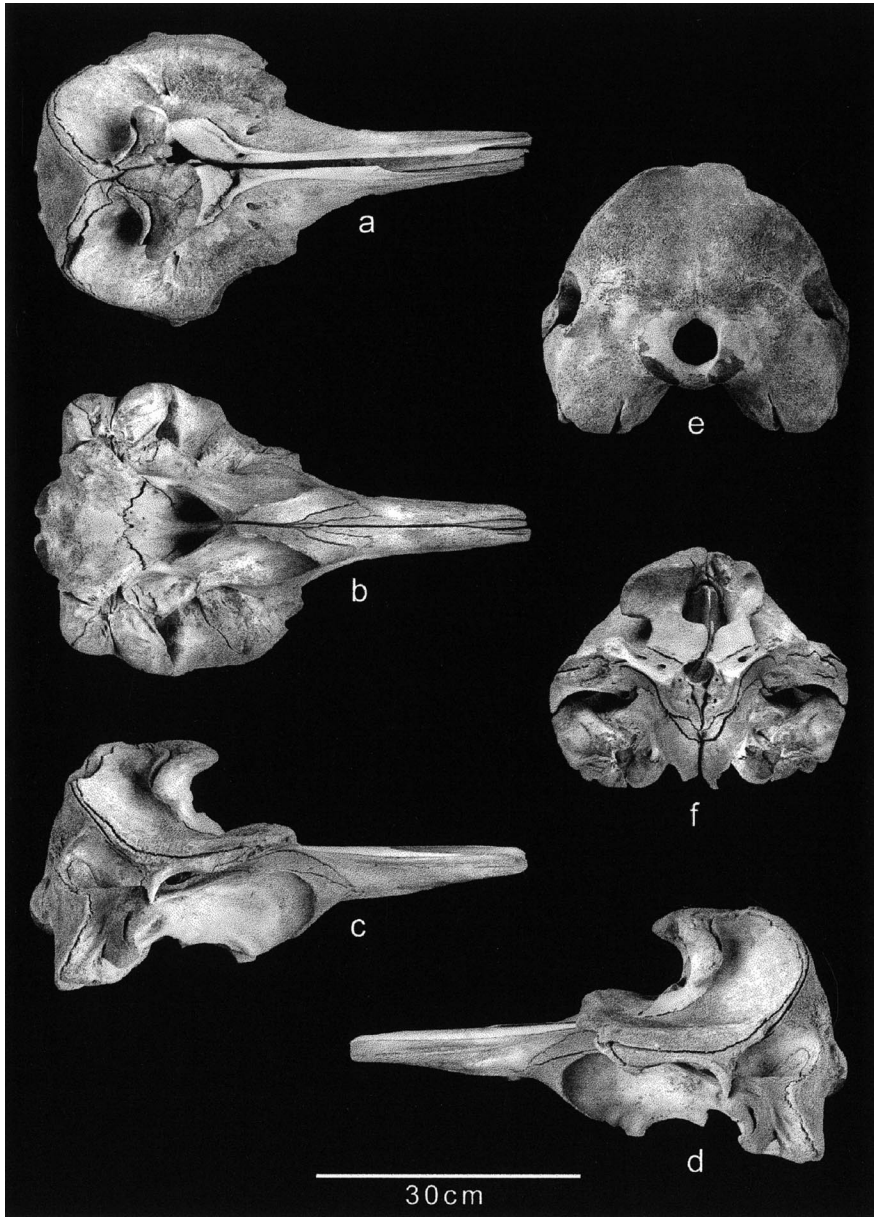


Figure 4. Views of the White Island calvaria: (a) dorsal, (b) ventral, (c) right lateral, (d) left lateral, (e) posterior, (f) anterior.

gomatic width in MNHNC 1156 and an estimated 68% in the White Island calvaria (see Reyes *et al.* 1995 and Moore 1972 for data on other species).

3. The least distance of the premaxillary foramina, 20 mm and 24 mm in the two known calvariae of *M. traversii*, is smaller than in similar-sized cal-

Table 1. Measurements of mandible and teeth of the holotype of *M. traversii* (NMNZ 546).

Measurements	mm
Length of right ramus	824
Greatest length of mandibular symphysis	263
Length from posterior end of mandibular symphysis to condyle	568
Length from anterior tip of mandible to mid-point alveolus (r)	289
Length from anterior tip of mandible to mid-point alveolus (l)	285
Length from posterior margin alveolus to condyle (r)	466
Length alveolus (r)	154
Length alveolus (l)	142
Greatest height right ramus (663 mm from anterior tip)	137
Outside height of mandible at mid-length alveolus (r)	60
Inside height of mandible at mid-length alveolus (r)	69
Height mandible at anterior margin alveolus (r)	69
Height mandible at anterior margin alveolus (l)	67
Height mandible at posterior margin alveolus (r)	75
Height mandible at posterior margin alveolus (l)	74
Height mandible at mid-length symphysis (r)	46
Height mandible at mid-length symphysis (l)	48
Height mandible at $\frac{3}{4}$ length symphysis (r)	64
Height mandible at $\frac{3}{4}$ length symphysis (l)	65
Greatest width alveolus (r)	22
Greatest width alveolus (l)	23
Width mandible at anterior margin alveoli	89
Width mandible at mid-length symphysis	65
Width mandible at three-quarters length symphysis	86
Greatest width across mandibular condyles (from reflected image)	414
Length right tooth	70
Height right tooth	233
Width right tooth	15.5
Height denticle right tooth	14
Length denticle base, right tooth	16
Length left tooth	68
Height left tooth	238
Width left tooth	15
Height denticle left tooth	12
Length denticle base, left tooth	17

variae of other *Mesoplodon* species (see Reyes *et al.* 1995 and Moore 1972 for data on other species).

The mandible of NMNZ 546 (the measurements of which are given in Table 1) is incomplete: the left ramus is broken at mid-length, whereas on the right ramus the lower posterior corner below the condyle is missing. The anterior portion of the mandible is strong and the symphysis is long and deeply sunken medially. The alveoli straddle the posterior end of the symphysis. The alveoli are long, to accommodate the teeth which recline posteriorly at an angle of 140° , and are only slightly raised above the anterior portion of the jaw. As the teeth are very large and had clearly erupted in life, we assume that this animal was a male. This assumption is based on the strong

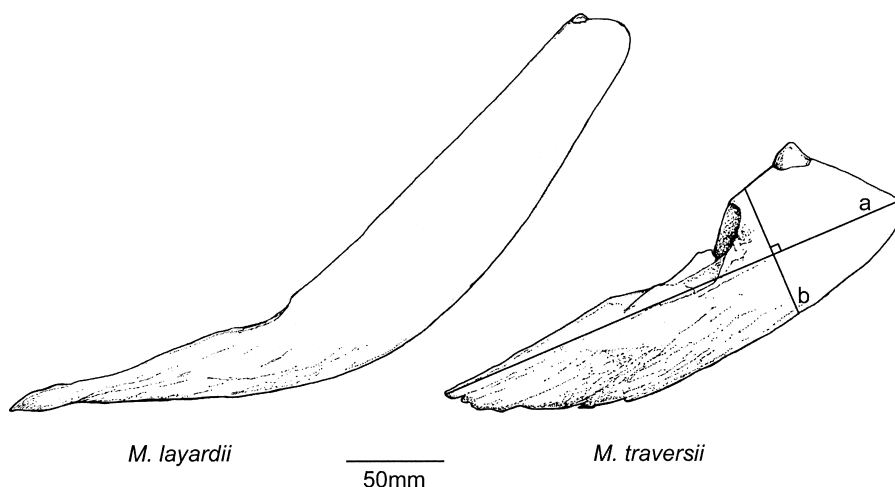


Figure 5. Diagram of left tooth of *M. traversii* showing where measurements of teeth were taken: (a) height, greatest distance between most extreme points on margin of tooth (measured from base); (b) length, greatest distance between margins of tooth perpendicular to height of tooth; width is greatest thickness taken laterally through tooth horizontally at right angles to length (not depicted). A drawing of a typical male *M. layardii* is given for comparison.

sexual dimorphism in tooth development observed for other *Mesoplodon* species (e.g., Moore 1968, Baker 2001). As the roots of the teeth are fully ossified, we believe that this animal was a fully mature adult. Although Hector's (1873) illustrations of this specimen are good, we present photographs here of the mandible and teeth to complete the record (Fig. 1).

The teeth are weakly sinusoidal in the sagittal plane, and the root is offset at about 20° . There is a large, prominent denticle on the apex of each tooth. This denticle is inclined forwards, with its tip facing outwards. The anterior margin of each tooth is severely eroded just above the gum line as seen in some other *Mesoplodon* species where the males have protruding tusks which impinge against the rostrum (e.g., *M. stejnegeri*; Yamada 1996; other *Mesoplodon* species; van Helden, unpublished data). As noted by Gray (1874), the teeth of *M. layardii* are more slender than those of *M. traversii*. It is likely that Gray's (1874) statement about *M. layardii* refers to the smaller horizontal length of the exposed tooth while it is *in situ* in the mandible. Although the greater horizontal length in the teeth of *M. traversii* is an obvious visual distinction between the two species, it is not easily defined as a measurement. Therefore, we have described the teeth according to the measurements shown in Figure 5 (see Table 1). The teeth of adult male *M. layardii* taper towards the tip, clearly distinguishing them from *M. traversii* (see Fig. 5) The length of the tooth in *M. traversii* gives it a broad spade-like appearance compared to the narrower strap-like appearance of the teeth in *M. layardii*. Overall, the terminal length and large denticle are especially distinctive for *M. traversii*.

The greater amount of comparative material of mature male *M. layardii*

specimens now available (six in NMNZ) demonstrates consistency in the shape of the teeth and mandible of this species, confirming Gray's observation of the differences between *M. layardii* and *M. traversii*.

DISCUSSION

Our results combine morphological and molecular evidence to unify three fragmentary and disparate museum-held beaked whale specimens resulting in the synonymy of *M. babamondi* with *M. traversii*. This multidisciplinary approach has provided new insight into the distribution and distinctiveness of what is arguably the least known of all living species of cetacean.

The rediscovery of *Mesoplodon traversii* brings the total number of ziphiid species known from New Zealand waters to eleven, and the number of species first described from this area to five (*Tasmacetus shepherdi*, *M. bowdoini*, *M. grayi*, *M. hectori*, and *M. traversii*). This suggests that the New Zealand region may be the richest in the world in terms of beaked whale species diversity.

Common Name

No common name was suggested by J. E. Gray so we propose *M. traversii* to be known as the spade-toothed whale (English), zifio de Travers (Spanish), baleine à bec de Travers (French) and spade-tand spitsssnuitdolfijn (Dutch). These names refer, respectively, to the extraordinary shape of the tooth, which is reminiscent of the oblong blade of the flensing knife (known as a "spade") used by North American whalers in the 19th Century, and to Henry Hammersley Travers Esq. (1844–1928), a Victorian lawyer who was sent to the Chatham Islands by his father to collect botanical and ethnographic items and who brought back the holotype specimen. By referring to the tooth in the common name it is hoped that people will become aware that there is more than one species of *Mesoplodon* with tall prominent teeth that bear a denticle.

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