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A Newly Recognised Beaked Whale (Ziphiidae) in the Tropical Indo-Pacific: *Mesoplodon hotaula* or *M. ginkgodens hotaula*

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Abstract
We present genetic and morphological data supporting the recognition of a previously described but unrecognised *Mesoplodon* beaked whale in the tropical Indo-Pacific. Currently known from at least seven specimens (Sri Lanka [1], Kiribati [1+], Hawai'i [3], Maldives [1], Seychelles [1]), this beaked whale is the sister-taxon to *M. ginkgodens* proper. The type specimen (Sri Lanka) was described as a new species, *M. hotaula,* in 1963, but the species was subsequently synonymised with *M. ginkgodens* by Moore and Gilmore (1965). Analyses of three mitochondrial genes and eight nuclear introns, together with distinct morphological features, suggest that this specimen and the others we have identified as belonging to this lineage represent a distinct species or subspecies of beaked whale.

Introduction
For the majority of beaked whales (family Ziphiidae), most of what we know has come from beachcast or stranded animals (Reeves et al., 2002). To assist with beaked whale identification and discovery, a comprehensive, validated DNA taxonomy for all known species in this group was established using sequences from mitochondrial DNA (mtDNA) control region (CR) and cytochrome *b* (CYB) genes (Dalebout et al. 2004, Dalebout et al. 2007). For the genus *Mesoplodon,* these markers showed consistently low intra-specific variation and comparatively high inter-specific divergence. In phylogenetic analyses, DNA sequences from each of the known species clustered together to the exclusion of sequences from the other known species. All species also possessed diagnostic nucleotide substitutions that appear to distinguish them from all other *Mesoplodon* species (though it is recognised that the small sample sizes available may lead to underestimates of intra-specific variation). These results were in concordance with morphological diagnoses. Previous application of this DNA taxonomy has resulted in several significant findings: the description of a new species from the North Pacific (*M. perrini*; Dalebout et al. 2002); the resurrection of a long-forgotten species in the Southern Hemisphere (*M. traversii*; van Helden et al. 2002); and confirmation of the identity of the enigmatic "tropical bottlenose whale" (*Indopacetus pacificus*; Dalebout et al. 2003).

This DNA taxonomy therefore offers a robust framework within which the discovery of a divergent lineage could indicate the existence of an unrecognised species or subspecies. Just such a lineage was reported by Dalebout et al. (2007), represented by several specimens which appeared to be closely related to *Mesoplodon ginkgodens* Nishiwaki and Kamiya 1958. Further specimens representing this divergent lineage have since been discovered. One of these is a specimen from Sri Lanka described as a new species, *M. hotaula* (Deraniyagala 1963a,b)[1] but subsequently synonymised with *M. ginkgodens* by Moore and Gilmore (1965). *M. ginkgodens* is one of the rarest of beaked whale species. It is known from less than 30 strandings and there has yet to be a confirmed sighting in the wild (MacLeod et al. 2006). Given the few records to date and the fact that they are all strandings, little can be said about comparative distributions. However, the divergent "*M. hotaula*" lineage appears to be tropically distributed, while strandings of the other lineage, *M. ginkgodens* proper, have generally been in more temperate regions (Fig. 1). To assess the taxonomic status of this divergent lineage, DNA from three mitochondrial genes and eight nuclear introns, as well as morphological characters, were analysed.

[1] There is no evidence that Deraniyagala was aware of the existence of *M. ginkgodens* when he described *M. hotaula*.

Methods

Material Examined

Seven specimens of *M. hotaula* were examined (Table 1) and compared to all other known *Mesoplodon* species using phylogenetic analyses of mtDNA and nuclear gene sequences. (The initial conclusions of Dalebout et al. (2007) were based on mtDNA analyses of specimens 2 – 4). Museums and institutions holding specimens of *M. hotaula* are as follows: the National Museum, Colombo, Sri Lanka (n = 1), Smithsonian National Museum of Natural History, Washington DC, USA (USNM, n = 3), a private collection in the Republic of Maldives (n = 1), and the Island Conservation Society, Seychelles (n = 1). Specimen 2 from Kiribati is known only from a soft tissue sample held in the University of Auckland DNA and Tissue Archive, Auckland, New Zealand (see SC/64/SM4 Baker et al. for information on additional specimens represented by osteological material from this region). Genetic and morphological comparisons were made to six specimens of *M. ginkgodens* (Table 1), including the holotype (Nishiwaki and Kamiya 1958). For genetic comparisons to other *Mesoplodon* species, up to six specimens per species were sampled (see Dalebout et al. 2007 for details).

Genetic Analyses

The Polymerase Chain Reaction (PCR) was used to amplify fragments from three mitochondrial genes (control region – CR, cytochrome *b* – CYB, cytochrome oxidase I – COI), seven nuclear autosomal introns (biglycan – BGN, catalase – CAT, rhodopsin – RHO, cytotoxic T-lymphocyte-associated serine esterase 3 – CTLA3, cholinergic receptor-nicotinic alpha polypeptide 1 – CHRNA1, muscle actin ACT, major histocompatibility complex class II – DQA) and one nuclear Y-chromosome intron (DBY7). For all details laboratory procedures and genetic analyses, see Dalebout et al. (2004) and Dalebout et al. (2008), or contact the lead author.

Results

Genetics

Mitochondrial DNA – CR fragments (658 bp) were successfully sequenced from all seven specimens of *M. hotaula.* CYB fragments (384 – 706 bp) were successfully sequenced from only four specimens due to degraded nature of much of the available material. A COI fragment (987 bp) was successfully sequenced from one specimen (Table 2). These mtDNA fragments were also successfully sequenced from up to six specimens of *M. ginkgodens.*

For mtDNA CR, comparisons between *M. hotaula* and *M. ginkgodens* revealed 35 variable sites, of which 18 appear to represent fixed differences between the species (Dα, net divergence 3.6% ± 0.91%). In comparisons including all *Mesoplodon* species, Dα ranged from 3.1 % to 8.3%. For mtDNA CYB, comparisons between *M. hotaula* and *M. ginkgodens* revealed 31 variable sites, of which 26 appear to represent fixed differences between the species, including 4 non-synonymous substitutions (Dα, net divergence 8.2% ± 1.79%). In comparisons including all other known *Mesoplodon* species, Dα ranged from 5.5% to 16.6%. For mtDNA COI, comparisons between *M. hotaula* and *M. ginkgodens* revealed 64 variable sites, of which 49 appear to represent fixed differences between the species (Dα, net divergence 5.5% ± 0.76%). In comparisons including a subset of *Mesoplodon* species (*M. mirus, M. europaeus, M. densirostris*), Dα ranged from 5.5% to 10.0%.

Intra-specific diversity for *M. hotaula* at the mtDNA CR and CYB was low, in line with trends observed in other *Mesoplodon* species. For CR, the Pacific Ocean specimens (Kiribati and Hawai'i) shared the same haplotype, while the Indian Ocean specimens (Sri Lanka, Maldives, Seychelles) differed from this by 3 – 7 bp. For CYB, the Pacific Ocean specimens differed from one another by 1 bp, while the only Indian Ocean specimen sequenced for this locus to date (Seychelles) differed from this by 4 – 5 bp.

In phylogenetic analyses of the combined mtDNA CR and CYB sequences (819 bp) including all known *Mesoplodon* species, the *M. hotaula* and *M. ginkgodens* specimens clustered together in two strongly-supported, species-specific clades (bootstrap scores 100%, posterior probabilities 1.00) which were reciprocally monophyletic to one another (Fig. 2). The sister-species relationship of these taxa was also strongly supported (bootstrap 91%, posterior probability 1.00). All other *Mesoplodon* species formed similar strongly-supported, species-specific clades, with branch lengths reflecting the relatively low genetic diversity observed *within* species and the comparatively large genetic divergence observed *between* them (see also Dalebout et al. 2002, Dalebout et al. 2004, Dalebout et al. 2007). Individual analyses of the CR and CYB datasets revealed the same pattern (Dalebout et al. 2007).

Nuclear introns – Intron fragments were successfully amplified from seven autosomal genes: BGN, 706 bp; CAT, 559 bp; RHO, 166 bp; CTLA3, 305 bp; CHRNA1, 366 bp; ACT, 925 bp; and DQA, 456 bp. Due to degraded nature of much of the material available, each species was represented by only a single specimen for these analyses. Over all these introns combined (3348 bp), all *Mesoplodon* species analysed, including the *M. ginkgodens-M. hotaula* complex, possessed nucleotide substitutions that distinguished them from all other *Mesoplodon* species (Table 3; see also Dalebout et al. 2008). Further, *M. ginkgodens* also possessed one nucleotide substitution that distinguished it from *M. hotaula* and all other *Mesoplodon* species.

Intron fragments were also successfully amplified from one Y-chromosome gene (DBY7, 241 bp). Due to degraded nature of much of the material available and the male-only nature of this marker, each species was again represented by only a single specimen. Our inclusion of data from this marker has several advantages. First, under random mating, the effective population size of this non-recombining chromosome is ¼ that of single copy autosomal markers such that the accumulation of mutations through genetic drift occurs far more rapidly. Second, the Y-chromosome is exposed to mutations that have arisen only in the male germline, giving us a male-specific marker to compare to the female-specific mtDNA markers. For DBY7, the majority of *Mesoplodon* species sampled, including *M. hotaula* and *M. ginkgodens*, possessed at least one nucleotide substitution that distinguished them from all other species in this genus (Table 4). Only one other sister-species pair (*M. bowdoini* and *M. carlhubbsi*; e.g., Dalebout et al. 2008) was included in these sex chromosome analyses. However, unlike *M. ginkgodens* and *M. hotaula*, these species did not possess any nucleotide substitutions at this locus that distinguished them from one another.

Morphology

Diagnostic features

The following characters of the teeth and skull are, when combined, diagnostic for *M. hotaula* (Fig. 3).

1) Single pair of large, laterally-compressed mandibular teeth, posterior to mandibular symphysis.
2) Teeth with vertical growth form, taller than they are wide, not symmetric; posterior margin convex, anterior margin almost planar.
3) Greatest transverse span of combined premaxillary bones ≥ 60 mm and 'flattened' in cross section.
4) Short mandibular symphysis (distal portions of mandibles appear 'stubby').

Feature 1 is shared with *M. ginkgodens, M. bowdoini,* and *M. densirostris*. Features 2, 3, and 4 distinguish *M. hotaula* from *M. ginkgodens*. Tooth form is particularly distinct. In contrast, the teeth of *M. ginkgodens* are wider than they are tall, both posterior and anterior margins are convex, and they are nearly symmetrical. For *M. ginkgodens,* the greatest transverse span of the combined premaxillary bones at the midpoint of the length of the beak is greater than 40 mm but less than 60 mm (diagnostic feature 5; Moore and Gilmore, 1965). Further, the premaxillary bones of *M. ginkgodens* are angled upwards (approx. 30 – 45º) rather than flattened (approx. 10 – 15º) as in *M. hotaula.* Adult male *M. ginkgodens* also appear to be larger in size (total length, 472 – 496 cm) than adult male *M. hotaula* (total length, 386 – 432 cm; Table 1). Full details of skull, mandibular, and external measurements, as well as photographs of all specimens, can be found in Dalebout et al. (in prep.).

Other morphological characters

Uniquely among currently recognised *Mesoplodon* beaked whales, adult males *M. ginkgodens* do not become heavily scarred with white, linear tooth rakes. This suggests that male:male competition in this species does not involve the use of the tusk-like teeth as weapons in combat, as has been inferred for other *Mesoplodon* beaked whales (e.g., Heyning 1984; Dalebout et al. 2008). Concordant with this observation, the mesorostral canal of adult male *M. ginkgodens* does not become ossified (filled in by vomer) as in most other *Mesoplodon* species. *M. hotaula* shares these characteristics with *M. ginkgodens* – i.e., no tooth rake scars and no infill of the mesorostral canal. Interestingly however, the teeth of two of the *M. hotaula* males were nonetheless extensively worn or broken (Fig. 5). It is not clear what could have caused this.

The only information we have to date on the external appearance of *M. hotaula* comes from the Seychelles adult male (Fig. 5). Preliminary analyses suggest that the colour pattern may also be distinct from that of *M. ginkgodens* (Dalebout et al. in prep.).

Discussion

There are many definitions and much debate around the topic of what constitutes a distinct 'species'. A specialist Workshop on Shortcomings in Cetacean Taxonomy (Reeves et al. 2004) concluded that the Genealogical Concordance Species Concept (GCC) would best suited for this challenging group of animals. Under the GCC, a group of organisms is considered to constitute a distinct species when the following criteria are met: 1) concordance across sequence characters within a genetic locus leading to conclusive exclusion; 2) concordance in these genealogical patterns across multiple loci, both mitochondrial and nuclear; 3) concordance with biogeographical patterns; and, 4) concordance with morphological characters. Overall, there must be evidence of 'irreversible evolutionary change' (Reeves et al. 2004). The GCC has subsequently been used by several authors to recognise previously synonymised species (Dalebout et al. 2004; Caballero et al. 2007).

The information we have presented here for *M. hotaula* meets many of the criteria of the GCC. *M. hotaula* is genetically (mitochondrial and nuclear) and morphologically distinct from *M. ginkgodens*, and the differences between these lineages are of a similar degree to those observed between other recognised *Mesoplodon* species. Further, *M. hotaula* occurs in both the tropical Indian and Pacific Oceans, while *M. ginkgodens* may occur only in the Pacific. Of the few records for *M. ginkgodens* in the Indian Ocean, we have demonstrated that the majority are in fact *M. hotaula.*

Of the other known Indian Ocean strandings, the Malacca, Malaysia specimen (November 1954) held by the Natural History Museum, London (BMNH) also appears to represent *M. hotaula* based on cranial morphology. In conclusion, we argue that *M. hotaula* represents a new subspecies (*M. ginkgodens hotaula*), if not a distinct species (*M. hotaula* Deraniyagala, 1963) in its own right.

The issue of taxonomic ranking will only be settled when more molecular and morphological data on the range of individual variation in both forms becomes available. Given that it has taken over 50 years to accumulate seven samples of one lineage and six of the other, it seems unlikely that numerous fresh specimens will become available in the foreseeable future. Therefore, additional ways of obtain nuclear data from existing bones and other degraded material should be pursued, even though this is likely to be challenging ; SNPs (single nucleotide polymorphisms) may be one possibility. Finally, we note the recent findings of bones representing additional specimens of the putative *M. hotaula* from the Gilbert Islands, Republic of Kiribati (Baker et al. SC/64/SM4) and detection of vocalizations that might represent *M. hotaula* from around Palmyra Atoll (Baumann-Pickering et al. 2010). These 'hotspots' may offer potential opportunities for collecting biopsy samples in the wild.

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Table 1. Specimens examined for this study. See text for details of museum holdings. H, holotype.

Specimen code	Other codes	Date found	Location	Coordinates	Total length (cm)	Sex
Mesoplodon hotaula						
1 3WZS (H)		1963 January 26	Ratmalana, Sri Lanka	6° 49' N, 79° 52' E	445	F
2 UKIRI		2003 July 11	Tabiteuea Atoll, Kiribati	1° 07' S, 174° 40' E[a]	?	M[b]
3 USNM593418	SW53473, PANWR12533-06001[c]	2005 November 9	Palmyra Atoll, Line Islands, Hawai'i	5° 52' N, 162° 06' W	480	F[b]
4 USNM593414	SW53474, PANWR12533-06002 [c]	2005 November 9	Palmyra Atoll, Line Islands, Hawai'i	5° 52' N, 162° 06' W	470	F?
5 USNM593426	SW70984, PANWR12533-06003 [c]	2006 July 8	Palmyra Atoll, Line Islands, Hawai'i	5° 52' N, 162° 06' W	386	M
6 MDV-X		2007 January?	Hulhudhuffaru, Raa Atoll, Maldives	5° 45' N, 73° 00' E	?	M
7 MM-0001		2009 June 20	Desroches Island, Seychelles	5°41′ S, 53° 39 E	432	M
Mesoplodon ginkgodens						
1 MginUSNM298237		1954 June 10	Del Mar, California, USA	32° 57' N, 117° 15' W	?	F
2 MginTSM8744 (H)	NSMT M8744	1957 September 22	Oiso, Tokyo, Japan	35° 18' N, 139° 18' E	472	M
3 MginMV29623		1983 June 26	Cape Reamur, Victoria, Australia	38° 23' S, 142° 08' E	?	?
4 MginTW01	NMNS-SU-94-29	1994	northeast coast, Taiwan	23° 46' N, 121° 0' E	?	F
5 MginNZ03	NMNZ2901	2003 April 10	Taranaki, New Zealand	39° 18' S, 174° 8' E	486	M
6 MginNZ04	NMNZ2618	2004 November 1	Pakawau, Nelson, New Zealand	40° 48' S, 172° 48' E	496	M

[a]Note that coordinates given in Dalebout et al. (2007) were incorrect.
[b]Determined or confirmed by molecular sexing.
[c]US Fish and Wildlife Service Palmyra Atoll National Wildlife Refuge Accession Number.

Table 2. Summary of genetic data held. Auto; autosomal; CR, control region; COI, cytochrome oxidase I; CYB, cytochrome *b*; DBY7, sex intron; MtDNA, mitochondrial DNA.

			Mitochondrial genes			Nuclear introns	
	Specimen code	DNA obtained from	CR	CYB	COI	Auto	DBY7
Mesoplodon hotaula							
1	3WZS	osteological material	Y				
2	UKIRI	soft tissue	Y	Y	Y	Y	Y
3	USNM593418	osteological material	Y	Y			
4	USNM593414	osteological material	Y				
5	USNM593426	osteological material	Y	Y			
6	MDV-X	osteological material	Y				
7	MM-0001	soft tissue	Y	Y			
Mesoplodon ginkgodens							
1	MginUSNM298237	osteological material	Y				
2	MginTSM8744	osteological material	Y				
3	MginMV29623	osteological material	Y				
4	MginTW01	soft tissue	Y	Y	Y	Y	
5	MginNZ03	soft tissue	Y	Y	Y	Y	Y
6	MginNZ04 (NMNZ2618)	soft tissue	Y	Y	Y		Y

Table 3. Nuclear DNA. Summary of nucleotide substitutions ('diagnostic characters') distinguishing each *Mesoplodon* species from all other species in this genus over seven autosomal introns (BGN, CAT, RHO, CTLA3, CHRNA1, ACT, DQA; total 3348 bp) and one Y-chromosome intron (DBY7, 241 bp), *sensu* Davis and Nixon (1992).

Species	Autosomal introns[a] (3348 bp) # substitutions	Y-chromosome intron[b] (241 bp) # substitutions
M. bidens	13	1
M. bowdoini	4	0
M. carlhubbsi	8	0
M. densirostris	9	_
M. europaeus	11	2
M. ginkgodens-M. hotaula complex	4	2
M. grayi	1	1
M. hectori	9	1
M. layardii	6	1
M. mirus	10	0
M. perrini	5	1
M. peruvianus	6	_
M. stejnegeri	5	1[c]
Average	**7.3**	**1**
M. ginkgodens only	1	1
M. hotaula only	0	1

[a]Missing *M. traversii*
[b]Missing *M. densirostris, M. peruvianus, M. traversii*
[c]Insertion mutation (3 bp)

Figure 1. Stranding locations of *M. hotaula* (circles) and *M. ginkgodens* (triangles) specimens examined for this study. Diagonal lines represent the possible distribution of *M. ginkgodens,* as currently recognised (after Jefferson et al. 2008). Note however that there have been no records from the eastern South Pacific.

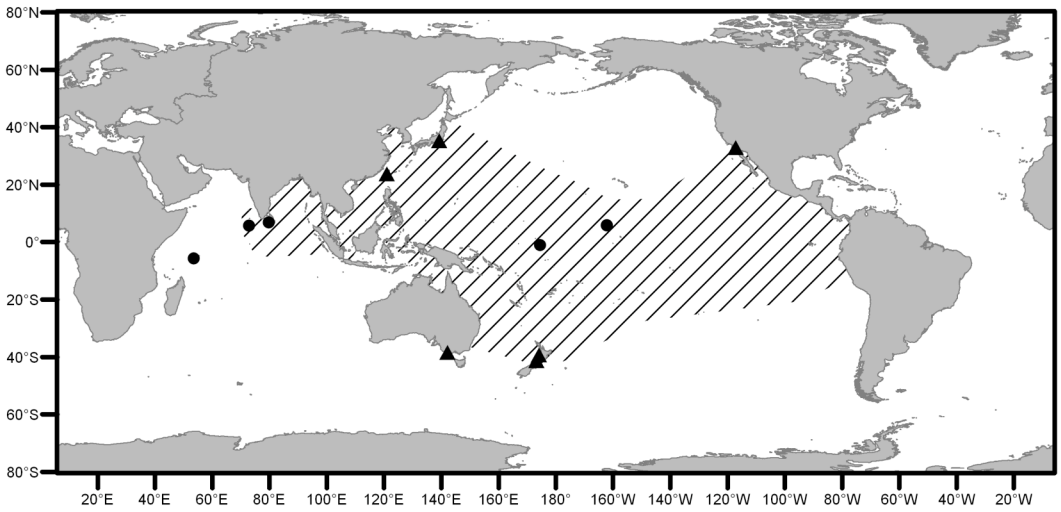


Figure 2. Maximum likelihood (ML) reconstruction of phylogenetic relationships among *Mesoplodon* beaked whales based on combined CR and CYB mtDNA sequences. Clade robustness is shown by bootstrap scores (≥ 60%, above branches) and Bayesian posterior probabilities (≥ 0.90, below branches). Note strong support of all species-specific groupings (majority of bootstrap scores > 80%, posterior probabilities > 0.95) and consistent patterns of low intra-specific genetic variation and high inter-specific genetic divergence in this group. Higher-level relationships between species were generally not well resolved by these markers (gray-shaded regions, most bootstrap scores <50%).

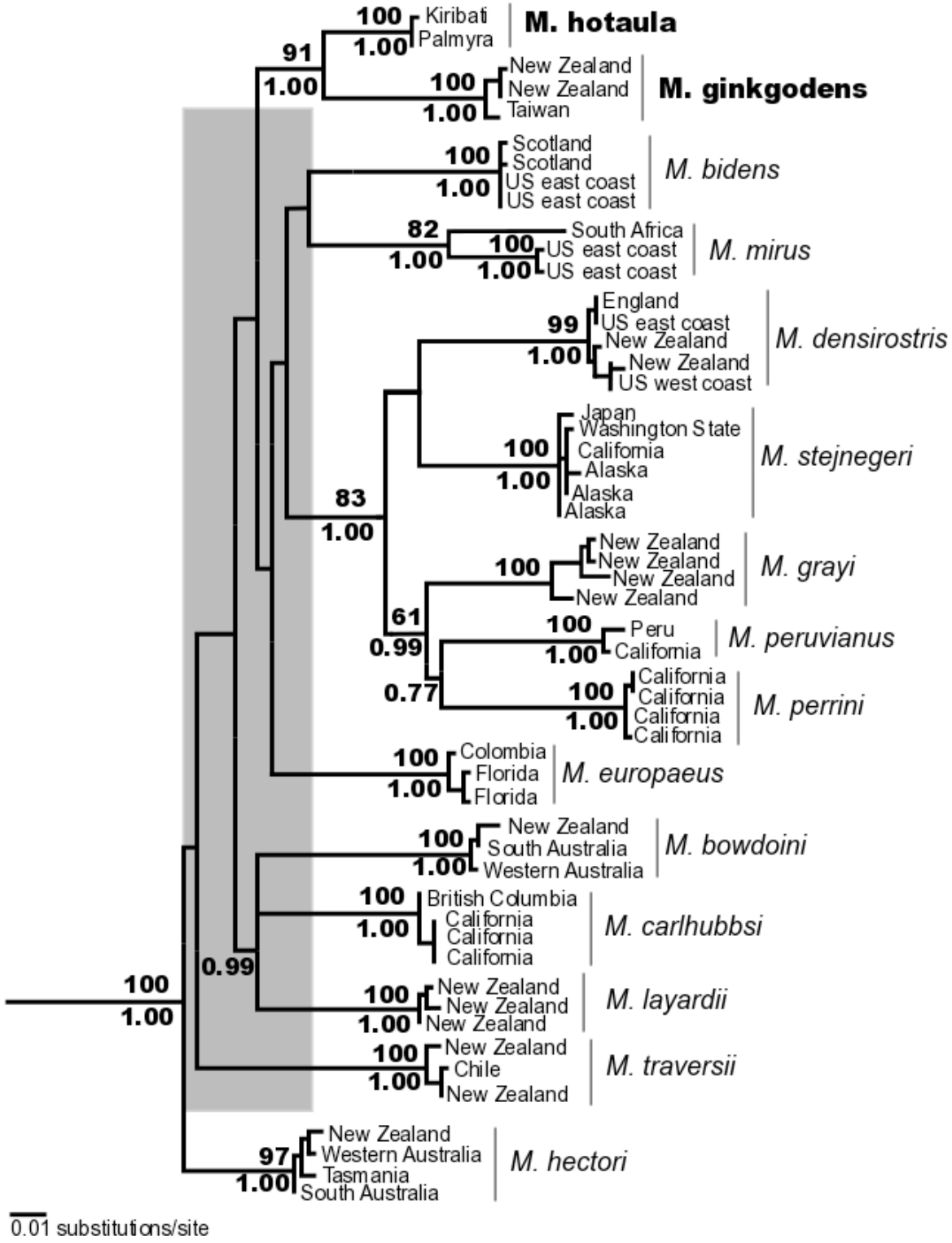
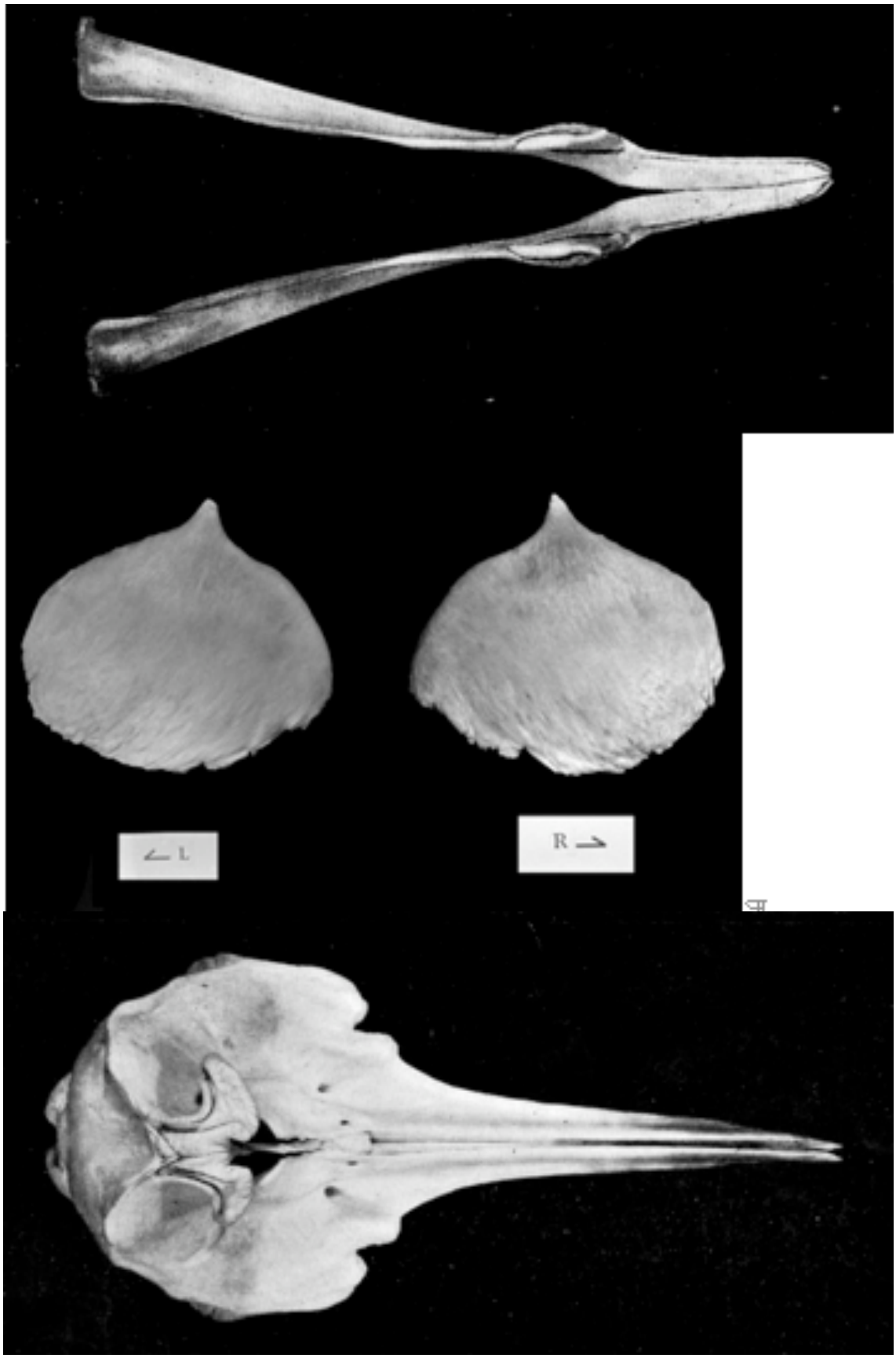


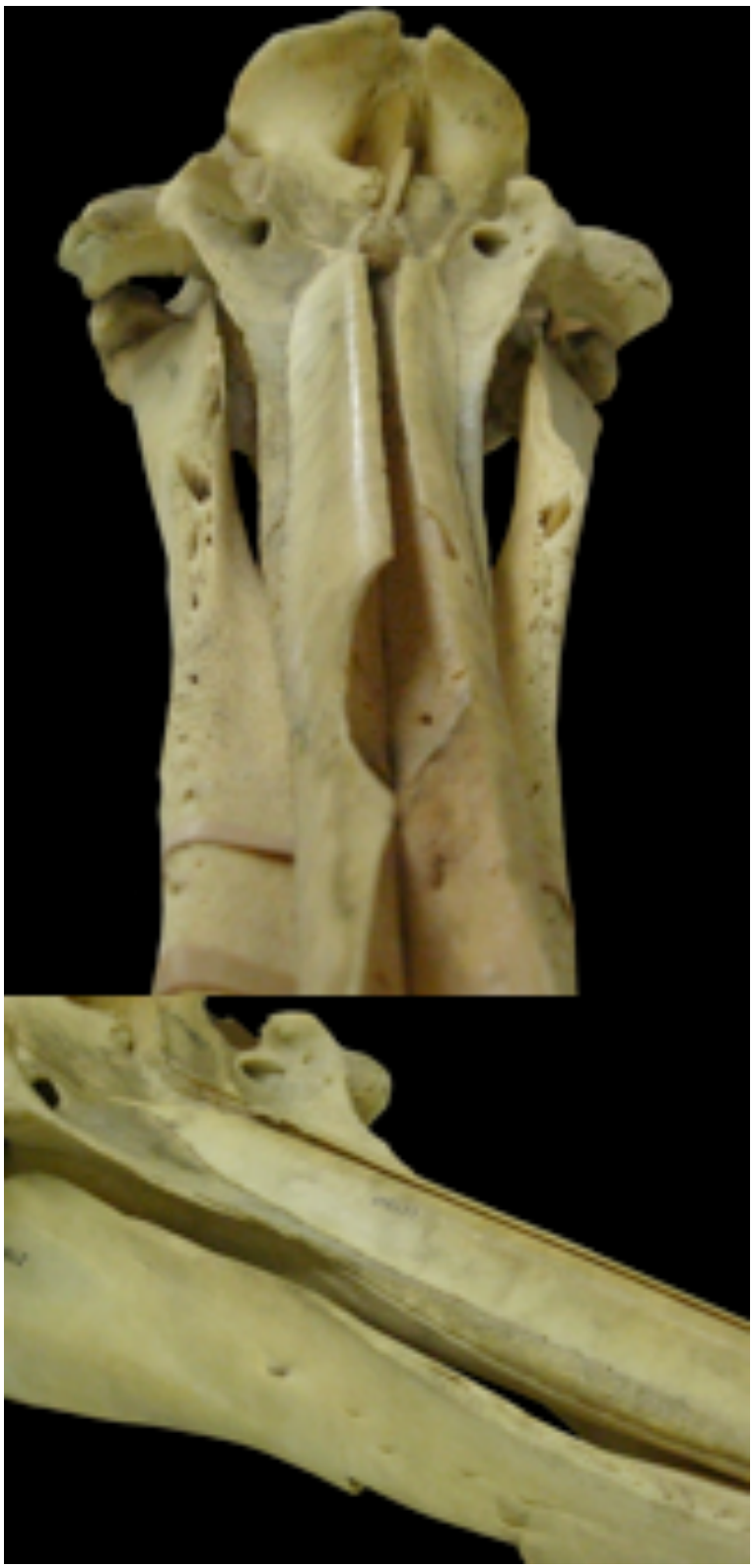
Figure 3. Morphological comparisons of *M. hotaula* and *M. ginkgodens*

A) *M. hotaula* adult male (Maldives, MDV-X).
Photocredit: R. Charles Anderson.

B) *M. hotaula* adult female (Hawai'i, USNM593418 and USNM593414).
Photocredit: Merel Dalebout.



C) *M. ginkgodens* adult male (Japan, TSM8744, holotype).
Image from Nishiwaki and Kamiya (1958).



D) *M. ginkgodens* adult female (California, USNM298237).
Photocredit: Merel Dalebout

E) *M. hotaula* adult male (Seychelles, MM001).
Photocredit: Lisa Thompson.

F) *M. ginkgodens* adult male (New Zealand, MginNZ04).
Photocredit: Hans Stoffregen, Department of Conservation, New Zealand.