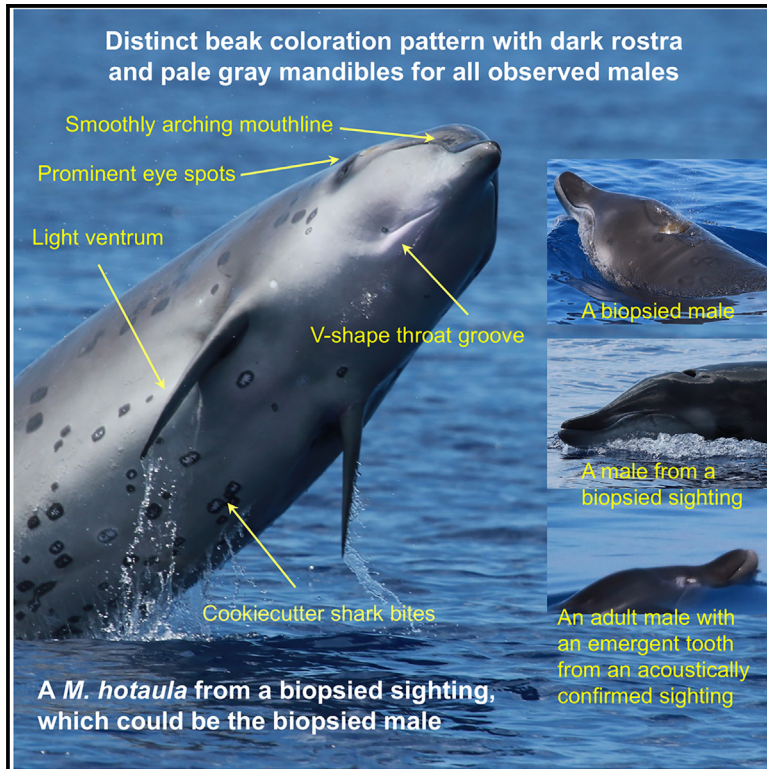


# Identification of the enigmatic Deraniyagala's beaked whale

## Graphical abstract



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## In brief

Marine organism; Ecology; Zoology

## Highlights

- Deraniyagala's beaked whale (*Mesoplodon hotaula*) is one of the least-known whales
- *M. hotaula* has distinguishing acoustic and morphological characteristics
- *M. hotaula* might be more widespread in distribution range than previously thought
- The South China Sea is a potentially important area for the *M. hotaula*



## Article

# Identification of the enigmatic Deraniyagala's beaked whale

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## SUMMARY

It is essential to discover and identify animals in species level in the wild to achieve the collection of baseline data and benefit better understanding and conservation of the rare species. However, this is far from being realized for many beaked whales in the deep sea, including the Deraniyagala's beaked whale (*Mesoplodon hotaula*), which is one of the least-known whales with no confirmed live sightings at sea yet all over the world. Here, we provide the first robust field identification of *M. hotaula*, by integrating DNA sequencing of skin biopsies, acoustic data, and photographs. Our discovery illustrates that *M. hotaula* has distinguishing acoustic and morphological characteristics, enabling us to distinguish it from other mesoplodonts in the wild. The identification of *M. hotaula* in species level is rapidly advancing our knowledge on its distribution range, habitat characteristics, behavior, ontogenetic color pattern development, group size and structure, and potential threats.

## INTRODUCTION

It is essential to identify animals at the species level in the wild to obtain baseline data on distribution, population size and structure, and life history, and to inform their management and conservation. However, this goal has yet to be realized for many beaked whales (Ziphiidae). The 24 recognized species of beaked whales represent this poorly known megafaunal family.<sup>1,2</sup> Their dolphin-shaped bodies, small group size, deep-sea habitat, and dives deeper than 1,000 m for tens of minutes or longer limit the opportunities to reliably identify and study them.<sup>3,4</sup> They, particularly mesoplodonts (*Mesoplodon* spp., the most speciose yet least known genus of cetaceans with 16 currently known species), also have similar external morphological features and are challenging to tell apart alive or dead.<sup>5</sup> Some mesoplodont species, such as the Deraniyagala's beaked whale (*Mesoplodon hotaula* Deraniyagala, 1963), are among the least-known whales and are often assigned only from decomposed, stranded specimens, with no confirmed live sightings at sea, and their field characteristics are largely or entirely unknown.<sup>2</sup> Their color patterning (also obscures with age in mesoplodonts) is problematic since the skin of stranded whales darkens quickly upon sun exposure. We now provide the first robust field identification of *M. hotaula*, by integrating DNA sequencing of skin biopsies, acoustic data, and photographs.

*Mesoplodon hotaula* was first described by Paulus Edward Pieris Deraniyagala in 1963 after an adult female washed ashore at Ratmalana, Sri Lanka<sup>6,7</sup>; however, only two years later, Joseph Curtis Moore and Raymond Maurice Gilmore synonymized *M. hotaula* with the ginkgo-toothed beaked whale

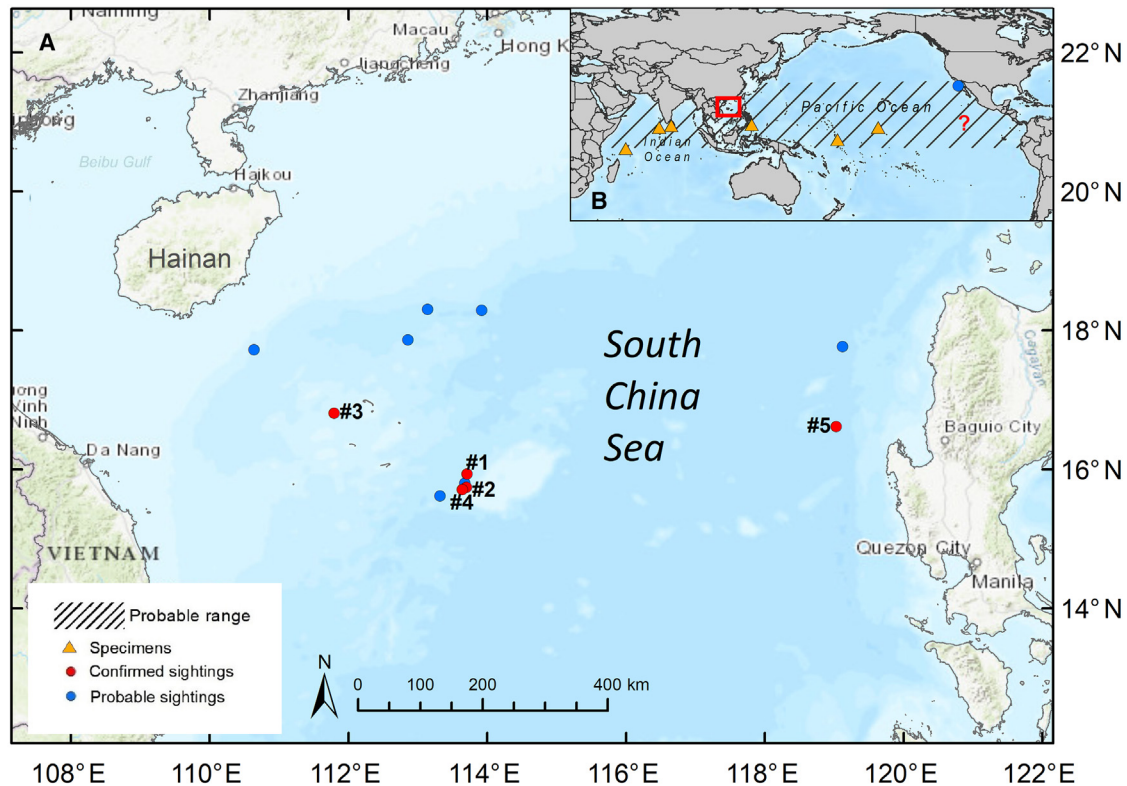
(*M. ginkgodens* Nishiwaki and Kamiya, 1958), since the former is like the latter in virtually every feature of the skull.<sup>8</sup> In 2014, morphological and genetic evidence from stranded individuals was used to resurrect *M. hotaula* as a species closely related to *M. ginkgodens*.<sup>9</sup> It was believed that accurate at-sea differentiation of *M. hotaula* from *M. ginkgodens* might not be possible due to their similar coloration, scarring patterns and possible overlapping ranges.<sup>10</sup> Information on the morphological appearance and distribution of *M. hotaula* stemmed from eight stranded specimens near remote islands of the equatorial Indo-Pacific (Sri Lanka, Kiribati, Seychelles, Maldives, Line Islands, and the Philippines),<sup>9,11–13</sup> with virtually nothing known about its life history and little information on its distribution.<sup>2</sup>

## RESULTS

### Description of sightings and collected data

During six ship-based surveys in the northern South China Sea between 2019 and 2023, primarily between April and September, we recorded 12 *Mesoplodon* sightings and identified five of them as *M. hotaula* (Figure 1A; Table 1; see details in three recent published papers<sup>14–16</sup>). Three dart-based skin biopsies of different *Mesoplodon* individuals were collected from two sightings (sightings #1 and #5 shown in Figure 1A; Table 1) and underwent DNA sequencing. Genetic analysis revealed that all the three biopsied *Mesoplodon* individuals were male *M. hotaula*. Frequency-modulated (FM) pulses were recorded from four sightings (sightings #1–4 in Figure 1A; Table 1), one of which (sighting #1) included two skin biopsies. Animals were photographed during 11 sightings including sightings #1–5





**Figure 1. Map showing sighting records and potential range of the Deraniyagala's beaked whale (*Mesoplodon hotaula*)**

(A) Sighting records of *M. hotaula* in the northern South China Sea. Confirmed sightings (red dots;  $n = 5$ ) correspond Table 1. Blue dots represent probable sightings ( $n = 7$ ).

(B) The probable range of *M. hotaula* estimated from confirmed specimens and probable sightings (map revised from Jefferson et al., 2015<sup>2</sup>). The waters east of Palmyra Atoll in the Pacific (e.g., Mexico and western South America) are marked as “?” i.e., questionable range for *M. hotaula*.

shown in Table 1 and other six probable *M. hotaula* sightings. The FM pulses recorded from the genetically identified *M. hotaula* (sighting #1) and three other acoustically similar sightings (sightings #2, 3, and 4) consistently showed a median peak frequency of around 43–46 kHz and a median interpulse interval (IPI) of around 207–270 ms. These pulses are different from other Ziphiidae species, including *M. ginkgodens*, suggesting they are from the same species: *M. hotaula*.<sup>15</sup>

### Morphological characteristics of *M. hotaula*

Photographs from individuals in a genetically identified sightings (i.e., sightings #5) had an estimated 3–5 m body length (Figure 2A), a prominent beak and forehead (Figure 2B), a brownish dorsum (Figure 2C), and acquired markings such as healed cookiecutter shark (*Isistius* spp.) scars (Figures 2C and 2D). The *M. hotaula* male juvenile, which was biopsied and genetically confirmed in sighting #5, lacked an erupted tooth (Figure 2B) and tooth-rake marks (Figure 2C). The juvenile shown in Figure 2D might be either the biopsied *M. hotaula* male or the group partner of the biopsied male (group size: 3). This individual (Figure 2D) showed a lightly pigmented ventral surface, prominent eye spots, a shallow V-shape throat groove, and a large number of small (sub)circular, dark scars, presumably from cookiecutter shark bites.

The adult male with an emergent tooth (Figure 3A), which was from sighting #2 and acoustically identified as *M. hotaula*, had an erupted tooth at the arch of its mouthline. Both two males i.e., one male (Figure 2B) from sighting #5 and the other from sighting #2 (Figure 3A), had an arched mouthline, pale cheek, a dark eye band separating two prominent white eye spots, and unique beak coloration (i.e., darker upper jaw). The *M. hotaula* calf (Figures 3B and 3C) identified from sighting #2 showed distinctive dorsal striping on its back, that is, the dark dorsal surface or cape mark in the calf extends from the melon or behind the blowhole to at least below the dorsal fin. This dorsal striping is absent in adults i.e., the *M. hotaula* adult male (Figure 3A; sighting #2) and the *M. hotaula* adult female (Figure 3C; mother from sighting #2), but obscured on the back of the *M. hotaula* juvenile male (Figure 2C; sighting #5).

Animals in the seven sightings without genetic or acoustic evidence showed similar morphological, behavioral, group size (1–4 individuals), and habitat characteristics, and are probable *M. hotaula* (Figure 1A). However, there was an exception, a juvenile individual from the acoustically identified sighting #2 with a flatter head and less arched mouthline (Figure 3D) compared to the *M. hotaula* calf (Figure 3E). It was morphologically identified as Blainville's beaked whale (*M. densirostris* Blainville, 1817). Therefore, sighting #2 was identified as a mixed-species

**Table 1. Brief summary of five confirmed *Mesoplodon hotaula* sightings in the South China Sea**

Sighting in Figure 1A	Observation date and period (UTC+8)	Acoustic recording period (UTC+8)	Acoustic detection period (UTC+8)	Species identification evidence	Group size
#1	August 17, 2021, 08:52–14:25	08:55–14:32, 16:26–06:30 (day+1)	10:15–10:15, 12:25–12:29	Acoustics, genetics, photographs, and visual observation	3 (including two genetically confirmed males)
#2	August 18, 2021, 08:29–12:55	08:35–13:09, 14:32–16:29, 18:30–06:30 (day+1)	10:21–10:51, 12:42–12:56	Acoustics, photographs, and visual observation	5 (including four <i>M. hotaula</i> individuals and one <i>M. densirostris</i> individual)
#3	August 22, 2021, 14:10–15:34	14:18–15:30, 21:00–05:30 (day+1)	14:42–14:48	Acoustics, photographs, and visual observation	3
#4	August 31, 2021, 11:35–12:59	11:35–14:45, 19:00–07:30 (day+1)	04:40 (day+1)–05:02 (day+1)	Acoustics and visual observation	2
#5	July 6, 2023, 11:34–14:53	11:41–15:28	11:58–12:08	Genetics, photographs, and visual observation	3 (including one genetically confirmed male)

group consisting of four *M. hotaula* individuals and one *M. densirostris* individual (Table 1).

## DISCUSSION

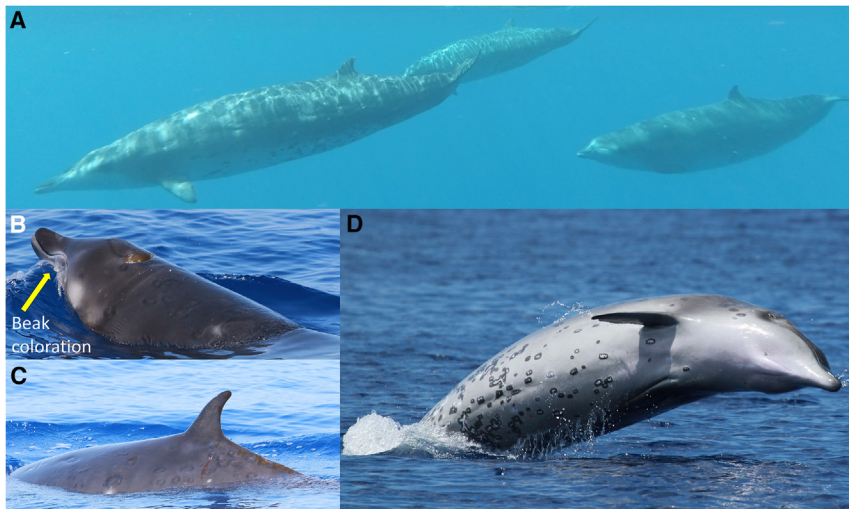
Our results illustrate that *M. hotaula* has distinguishing acoustic and morphological characteristics. Although its general appearance is superficially similar to other two mesoplodonts (*M. densirostris* and *M. ginkgodens*) inhabiting the Indo-Pacific waters, we identified two *M. hotaula* morphological features: (1) the shape of the mouthline (Figures 2B, 3E, and 4A–4H) and (2) the size, shape, and location of the erupted tooth in adult males (Figures 3A, 4A, 4C, and 4D). The only exception is *M. ginkgodens* (Figures 4I–4N), which shares these morphological characteristics with *M. hotaula*.<sup>10,14</sup> However, the adult male *M. hotaula* (Figures 2B, 2D, 3A, and 4A–4E) showed a distinct beak coloration pattern with dark rostra and pale gray mandibles compared to the white-tipped beak of adult male *M. ginkgodens* (Figures 4I–4L).<sup>2,9,14</sup> The dorsal striping pattern of young *M. hotaula* individuals (Figures 3B and 3C), which obscures with age (Figure 2C), may also be a distinguishing feature. This age-related feature has not been reported for *M. ginkgodens*, but a similar phenomenon was previously documented for Gervais’ beaked whale (*M. europaeus* Gervais, 1855) in the Atlantic.<sup>2,17</sup> The aforementioned two morphological characteristics<sup>14</sup> and the acoustic characteristics of its FM pulses<sup>15</sup> ensure that *M. hotaula* is distinguishable from other mesoplodonts including *M. ginkgodens* in the wild.

Our identification of one of the least known marine mammals highlights the value of DNA identification from biopsied samples in conjunction with acoustic recordings and photographs from the encountered sightings. The relative ease of live skin biopsies not only supports species and sex identification, but can also provide insights into geographic range, evolution, and phylogeny,<sup>16,18</sup> fast-tracking our understanding of the enigmatic beaked whales. This is also the first confirmed record that *M. hotaula* exists in the South China Sea. It represents the fifth beaked whale species recorded in Chinese waters, in addition to the previously recorded (mainly from stranding records) Cuvier’s (*Ziphius cavirostris* G. Cuvier, 1823), Blainville’s (*M. densirostris* Blainville,

1817), ginkgo-toothed (*M. ginkgodens*), and Longman’s (*Indopacetus pacificus* Longman, 1926) beaked whales.<sup>19,20</sup>

With the *M. hotaula* sightings reported here, a few previous stranding records and probable at-sea sightings near the South China Sea e.g., putative *M. hotaula* records in Malaysia, Thailand, Chinese Taiwan, and the Philippines, can now likely be attributed to *M. hotaula*.<sup>9,11,14</sup> Thus, the northern South China Sea and its neighboring waters are not only an *M. hotaula* habitat in addition to the equatorial Indo-Pacific,<sup>2,9</sup> but could also be recognized as a potentially important area for this species (see Figure 1B). These confirmed sightings of *M. hotaula* are the most northern records (close to 17°N) for this species. On a larger spatial scale, probable at-sea sightings and acoustic detections have also been made in other tropical areas such as the Palmyra Atoll, Line Islands, and Baja California.<sup>2,9,21</sup> While *M. hotaula* records are scarce, it might be more widespread than previously thought. Species identification information presented herein on *M. hotaula* will be expanded upon through continued deep-water and offshore surveys, in the study area and elsewhere, and may become more detailed. As more sightings can be confidently assigned as *M. hotaula*, our understanding of *Mesoplodon* distribution, ecology and life history parameters will improve and we may need to revisit what we think we know about these cryptic and hard to access species. As more dedicated surveys can be conducted, this species may quickly be moved from a species described as “virtually nothing is known of its life history”<sup>2,10</sup> to one of the well-studied mesoplodonts.

Deep diving cetaceans, such as the beaked whales, play a significant role in ecosystem functioning, not only through the popularized concept of carbon storage, but also as vertical transporters of nutrients from the depths to the sea surface, thus promoting primary productivity. There are huge gaps in our knowledge of beaked whales. The present study provides insights to accurate species identification, distribution and behavior. Given the role of deep diving cetaceans in ecosystem functioning and the ability and permitting in place in many areas to conduct deep sea mining, this study also provides data relevant to all marine ecologists who work in deep sea habitat, and provides information critical to impact assessments, which will



**Figure 2. Deraniyagala's beaked whale individuals from a genetically confirmed group**

(A) A genetically confirmed group of three *M. hotaula* individuals encountered on July 6, 2023, marked as sighting #5.

(B and C) Tissue sample was biopsied from one of the three whales, which was further confirmed as *M. hotaula* male by DNA analysis; (B and C) indicated the forehead, anterior, and dorsum sections of the genetically confirmed *M. hotaula* individual.

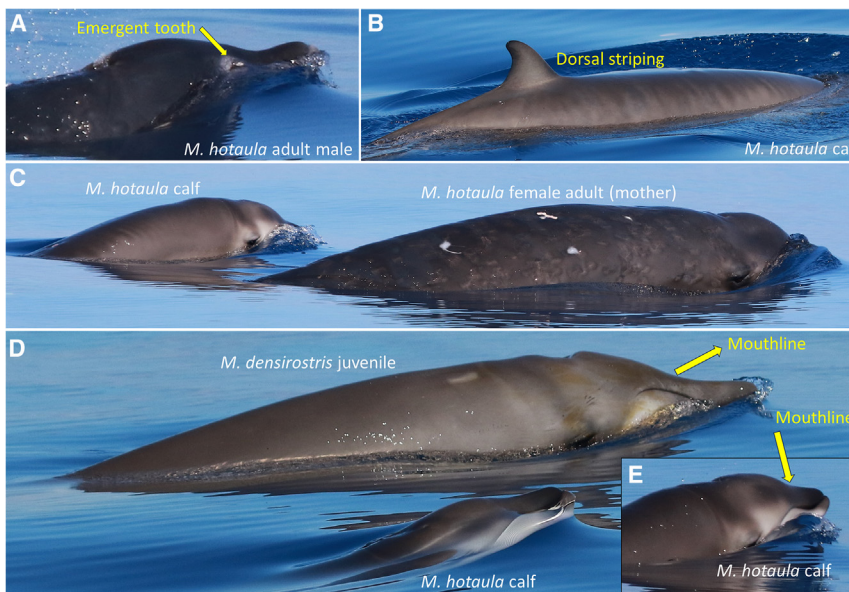
(D) The venter of one individual in this group showed lightly pigmented surface, prominent dark spots with a white center, clearly visible V-shape throat groove, and numerous cookiecutter shark bites. Notice the arched mandible, pale cheek, dark eye patch, dark flipper band, and beak coloration of the *M. hotaula* shown in (B), and (D). Photos: W. Lin and B. Liu, Marine Mammal and Marine Bioacoustics Laboratory, Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences.

be increasingly required as sea bed resource extraction activities spread.

Compared with land species, aquatic animals including megafaunal marine mammals are disproportionately poorly known.<sup>22</sup> The present discovery of *M. hotaula* in the South China Sea and recent revelation of several (possible) new species of beaked whales,<sup>23,24</sup> the giants of the oceans, also highlights how little we know about the ocean and its species diversity.<sup>1,25</sup> Advanced DNA technology in conjunction with accurate field observation, measurement, and sample collection is having a profound effect on our identification and understanding of the natural world including the marine world, where losses in biodiversity are unfortunately increasingly evident.

#### Limitations of the study

In this study, we reported a small number of *Mesoplodon* sightings ( $n = 12$ ), with only a few of them being genetically or acoustically confirmed as *M. hotaula* ( $n = 5$ ). The other seven was believed to be *M. hotaula* due to the proximity and similarity. However, this was not guaranteed due to overlapping ranging areas and similar external appearance of *M. hotaula* and *M. ginkgodens*. Moreover, notice that morphologic features and acoustic characteristics may show intra-specific variations across different survey regions. In the absence of genetic data, both of the morphologic and acoustic characteristics detailed in this study should be present before species can be confirmed. Therefore, special caution is necessary in future studies for *M. hotaula* identification and inter-species comparison,

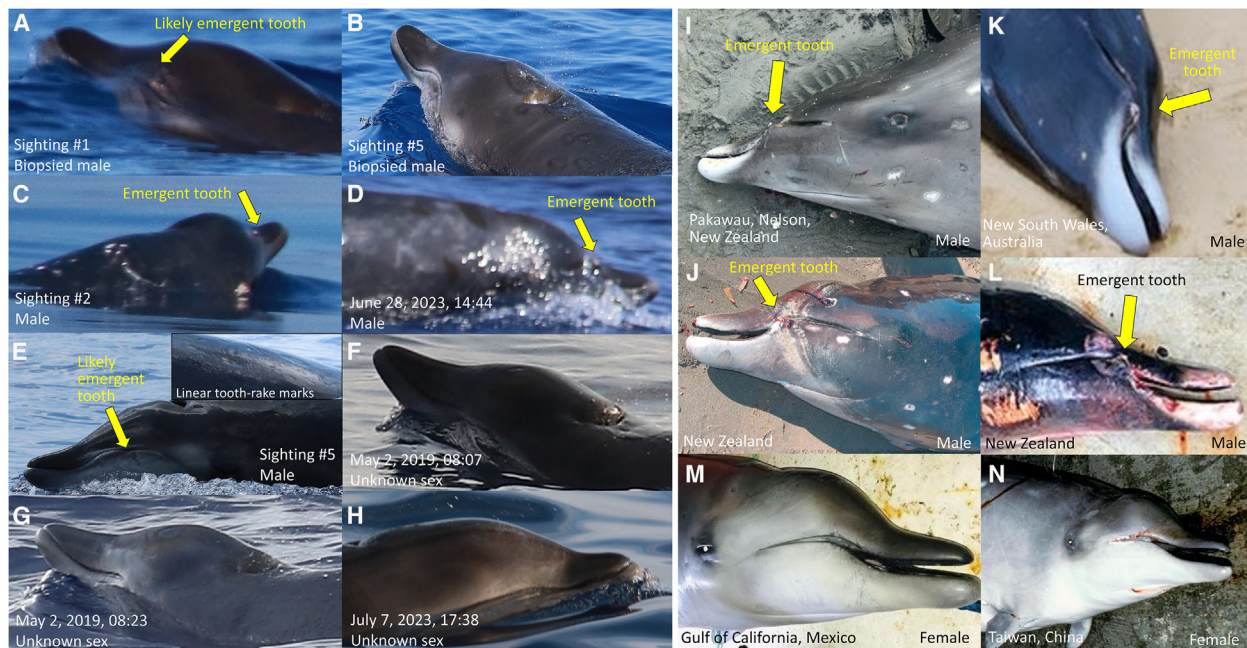


**Figure 3. An acoustically confirmed group of four *M. hotaula* individuals and an *M. densirostris* individual encountered on August 18, 2021, marked as sighting #2**

(A) A presumed adult male of *M. hotaula* with an emergent tooth.

(B) The *M. hotaula* calf shows distinctive dorsal striping on its back; (C) a pair of *M. hotaula* mother-calf; (D) synchronized swimming behavior of the *M. densirostris* juvenile and *M. hotaula* calf.

(D and E) Differences in the mouthline of *M. densirostris* juvenile and *M. hotaula* calf. Notice the beak coloration of the *M. hotaula* calf is similar to that shown in Figures 2B and 2D. Photos: W. Lin and B. Liu, Marine Mammal and Marine Bioacoustics Laboratory, Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences.



**Figure 4. Comparison of beak coloration between *M. hotaula* and *M. ginkgodens***

Comparison of beak coloration between (A–H) alive *M. hotaula* individuals in the South China Sea and (I–N) dead *M. ginkgodens* specimens in other regions. Animals shown in A–E are either genetically confirmed males or presumed males with emergent tooth or linear tooth-rake marks. Animals in (F–H) are unknown-sex individuals from those “probable” *M. hotaula* sightings in the South China Sea without enough acoustic or genetic evidence. Animals in (I–N) were genetically confirmed as *M. ginkgodens*, with four individuals (I–L) being identified as males and two (M and N) as females. Notice that *M. hotaula* individuals in (A–H) show a beak coloration pattern depicted as darker upper jaw than lower jaw. By contrast, the male *M. ginkgodens* (I–L) show a white beak tip for the anterior of both lower and upper jaws, while female *M. ginkgodens* in m and n show a dark pattern for the anterior of both upper and lower jaws. Photos: (A–H) W. Lin, B. Liu, and M. Lin, Marine Mammal and Marine Bioacoustics Laboratory, Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences; (I) H. Stoffregen, Department of Conservation; (J) B. Williams, courtesy of Department of Conservation; (K) M. Jarman, NSW Office of Environment and Heritage; (L) R. Suisted; (M) E. Rizo, courtesy Museo de Balena; (N) J. Wang.

especially when only one piece of species identification evidence is available.

#### RESOURCE AVAILABILITY

##### Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Songhai Li ([lish@idsse.ac.cn](mailto:lish@idsse.ac.cn)).

##### Materials availability

All materials including biological tissue samples, genetic data, acoustic recordings, and photographs in this study can be available from the [lead contact](mailto:lish@idsse.ac.cn), Songhai Li ([lish@idsse.ac.cn](mailto:lish@idsse.ac.cn)).

##### Data and code availability

- The published article includes all data generated and analyzed during this study.
- All *M. hotaula* genetic data used in this study have been made available in the China National GeneBank Nucleotide Sequence Archive (CNSA: <https://db.cngb.org/cnsa>; accession no. CNP0004483) and NCBI GenBank (accession no: OR754051-OR754056).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](mailto:lish@idsse.ac.cn) upon request.

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#### AUTHOR CONTRIBUTIONS

S.L. conceived and designed the study. S.L., M. Liu, W.L., L.D., and M. Lin collected the data. M. Liu, and S.L. analyzed and interpreted the data. S.L., M. Liu, and I.S. wrote the first draft of the manuscript. All authors contributed critically to manuscript preparation and gave final approval for its publication.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Animals ethics statement
- METHOD DETAILS
  - Fieldwork
  - Post-survey examinations

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
<b>Biological samples</b>		
Skin tissue samples	This paper	N/A
<b>Other</b>		
High-quality photographs and videos	This paper	N/A
Underwater sounds	This paper	N/A
Genetic data	This paper	China National GeneBank Nucleotide Sequence Archive (CNSA: <a href="https://db.cngb.org/cnsa">https://db.cngb.org/cnsa</a> ; accession no. CNP0004483) and NCBI GenBank (accession no: OR754051-OR754056)

### EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

#### Animals ethics statement

This work was performed with beaked whales in the wild under the ethical statement (No. IDSSSEYLL-MMMBL-01) approved by Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences, and the official permit (No. 2020-1726) approved by Hainan Provincial Department of Agriculture and Rural Affairs, People's Republic of China.

### METHOD DETAILS

#### Fieldwork

Between April 2019 and July 2023, we conducted six boat-based surveys targeting cetaceans in the South China Sea, primarily between April and September.<sup>14</sup> During these surveys, visual observations were implemented on the top deck of a 44-m research vessel to search for cetaceans.<sup>26,27</sup> Once cetaceans were encountered, we took high-quality photographs and videos using Canon 7D-II digital cameras, DJI Mavic pro drones, and GoPro underwater cameras.<sup>27,28</sup> When sea conditions were satisfactory, we recorded underwater sounds using SoundTrap 300HF recorders<sup>15,29</sup> and collected skin tissue samples from healthy adult animals using the Paxarms MK24C Projector biopsy sampling system.<sup>16</sup>

#### Post-survey examinations

In our acoustic datasets recorded from the *Mesoplodon* groups, we detected and extracted the typical echolocation clicks emitted by beaked whales, i.e., frequency-modulated (FM) pulses.<sup>15,29</sup> We compiled 23 available descriptions of FM pulses from the literature.<sup>30,31</sup> To compare the FM pulses produced by different *Ziphiidae* species, we performed hierarchical clustering with Euclidean distance on five acoustic parameters: peak frequency (kHz), center frequency (kHz), Teager-energy duration ( $\mu$ s), -10 dB bandwidth (kHz), and interpulse-interval (ms).<sup>18</sup> We extracted DNA from skin biopsy samples using the cetyltrimethylammonium bromide (CTAB) method,<sup>15</sup> and confirmed sex of the examined sample by PCR amplification of the male-specific SRY gene.<sup>9,32</sup> Three genetic markers (spanning the mitochondrial control region, the mitochondrial gene cytb, and the first intron of the nuclear muscle actin gene ACTA2) were used to compare our candidate *M. hotaula* samples to other Ziphiid sequences.<sup>9,16,32</sup>