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First record of Ramari's beaked whale *Mesoplodon eueu* (Cetacea: Ziphiidae) for Uruguay

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Abstract

We report the first record of Ramari's beaked whale (*Mesoplodon eueu*) from the temperate Southwestern Atlantic. Our analysis is based on an adult female and a plausibly associated calf/juvenile that stranded on the coast of Canelones Department, Uruguay. The species of the two individuals was identified via a combination of morphometric and molecular mitochondrial data and provide new insights into the Ramari's beaked whale, including previously unknown polymorphisms in the mitochondrial genome and a re-estimated date of divergence from *Mesoplodon mirus* at 2.5902 Mya.

Introduction

Beaked whales (ziphiids) are diverse and wide-ranging, yet remain poorly understood. *Mesoplodon* exemplifies this contradiction: with 16 members, it is the most speciose cetacean genus (Committee on Taxonomy, 2022) but also amongst the most enigmatic large mammals on Earth (Jefferson *et al.*, 2015). Notable knowledge gaps persist regarding species distributions, abundance estimates and even basic biology, with several species having never been recorded alive (MacLeod *et al.*, 2006; Pitman, 2018). *Mesoplodon* occurs from cold subpolar latitudes to the tropics, but can be difficult to observe owing to a preference for deep-water habitats (Reeves *et al.*, 2003; MacLeod *et al.*, 2006).

Ramari's beaked whale (*Mesoplodon eueu*, Carroll *et al.*, 2021) is the most recently described mesoplodont with records from South Africa, Australia, and Aotearoa New Zealand. Until recently, *M. eueu* was thought to be a southern, antitropical population of the North Atlantic True's beaked whale (*Mesoplodon mirus* True, 1913), but molecular and morphological data now confirm a deep independent history warranting species status (Ross, 1969, 1984; MacLeod *et al.*, 2006; Carroll *et al.*, 2021).

A previously reported stranding of True's beaked whale in Brazil also plausibly represents *M. eueu*, which may therefore range across the Southern Hemisphere (Souza *et al.*, 2005); however, to date no South American records of Ramari's beaked whale have been genetically confirmed. Here, we provide the first such record, based on two stranded individuals from Uruguay, and explore the implications of our new molecular data for the diversity and evolutionary history of the species.

Materials and methods

Our analysis is based on two beaked whales that stranded in Canelones Department, Uruguay, in 2019 (Figure 1). On 27th October 2019, the fresh carcass (Code 2 of Pugliares *et al.*, 2007) of a 338 cm long female calf/juvenile was found on San Luis Beach (34°46'31.6" S, 55°35'24.09" W; Figure 2). Three days later, a 528 cm long adult female washed up on Marindia Beach (34°46'48.19" S; 55°49'9.41" W), 24 km west from the first individual. This specimen showed a moderate state of decomposition (Code 3) suggesting that it died some time prior to the stranding (Figure 3).

Biological information and several photographs were recorded for both specimens. The skulls of both specimens along with muscle, blubber and skin samples and – for the second stranding only – the stomach contents were deposited at the National Museum of Natural History (Montevideo) under registration numbers MNHN 8211 and 8212, respectively. Tissue samples of both specimens were preserved in 95% ethanol and stored in a freezer at –20°C. As far as the position of the carcasses on the beach permitted, body measurements were taken following Norris (1961).



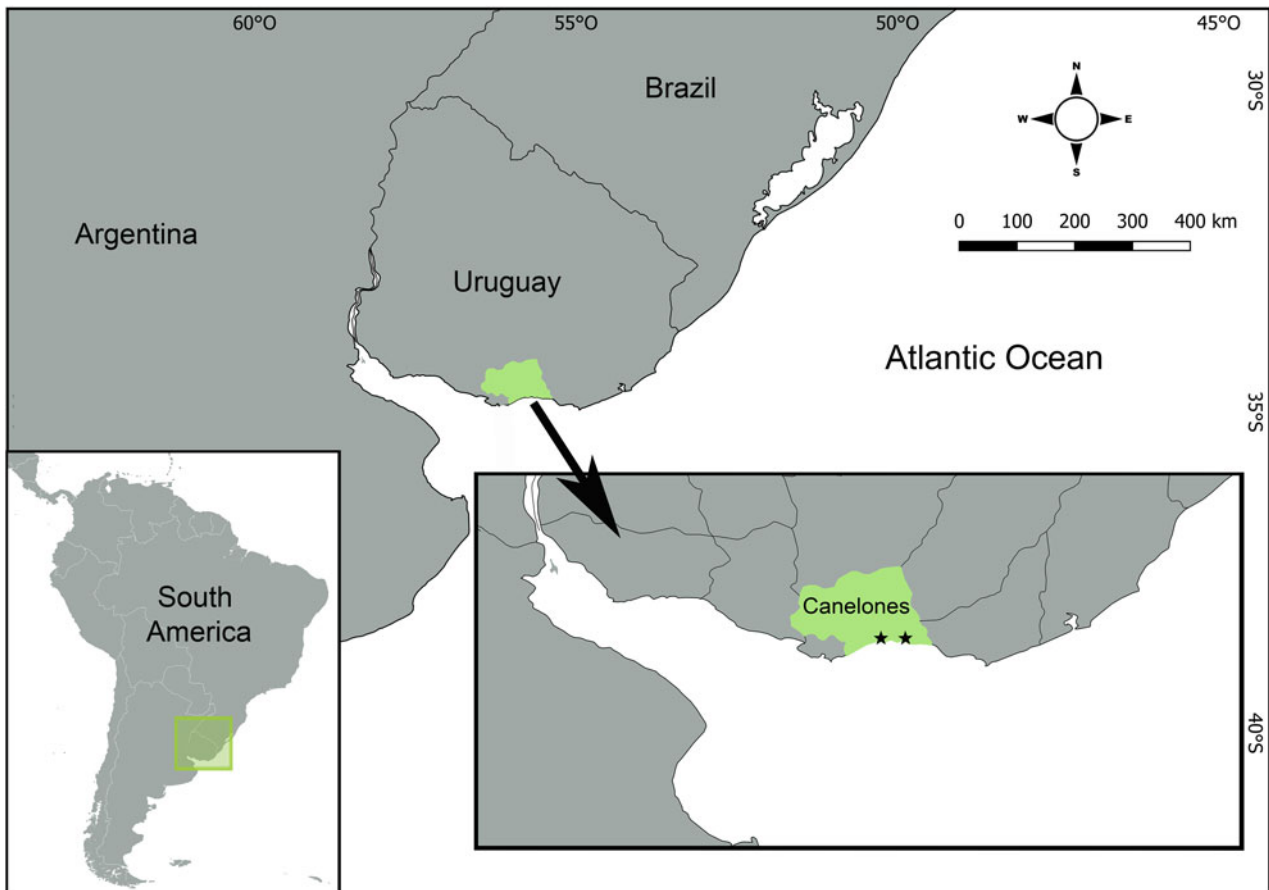


Figure 1. Location of the *Mesoplodon eueu* strandings in Canelones department (Uruguay), stars indicate the two stranding sites.



Figure 2. Left lateral view of the head (A) and ventral view (B) of a juvenile female of *Mesoplodon eueu* (MNHN 8211) stranded on the coast of Uruguay on 27th October 2019.



Figure 3. Dorsolateral view of an adult female *Mesoplodon eueu* (MNHN 8212) stranded on the coast of Uruguay on 30th October 2019.

Skull morphometrics

Following Carroll *et al.* (2021) we used eight measurements of the skull and mandible to test whether our individuals more closely resemble *M. eueu* or *M. mirus*. Measurements were taken to the nearest mm, adjusted for size by dividing them by the bizygomatic width, and log-transformed prior to further analysis. Finally, we combined our observations with those of Carroll *et al.* (2021) and summarized the entire dataset via principal component analysis (PCA) in PAST 4.03 (Hammer *et al.*, 2001).

DNA extraction, control region sequencing and genomic sequencing

Total genomic DNA was extracted from muscle following Medrano *et al.* (1990). The control region was sequenced using t-Pro (Dalebout *et al.*, 1998) and HS-5 primers (Okumura, 2004). The PCR cycling profile was the following: an initial denaturation at 94°C for 3 min, followed by 35 cycles of 94°C for 1 min, 60°C for 1 min, 72°C for 1 min, and a final extension at 72°C for 7 min. The amplified products were sequenced by MACROGEN (Seoul, Korea) using the Sanger sequencing method.

The genome of MNHN 8211 was sequenced on a DNBseq sequencing platform (BGITech Solutions, Hong Kong) using a 150 paired-end strategy and low coverage (1x \approx 2.5 Gb, genome size of Gervais' beaked whale *Mesoplodon densirostris*; Yuan *et al.*, 2021). Adaptor clean-up and quality filtering were performed by BGI. Mitogenome assembly was carried out using Novoplasty (Dierckxsens *et al.*, 2017) with the control region

sequence acting as a seed. In addition, we assembled the mitogenome of MNHN 8211 via Bowtie2 (Langmead and Salzberg, 2012), Samtools 1.10 (Li *et al.*, 2009) and Trinity v. 2.6.6 (Grabherr *et al.*, 2011), using the mitogenome of *M. eueu* (GenBank accession number OK326893) as a reference. Both mitogenome assemblies were congruent and the average coverage of the entire mitochondrial genome was 748. The average Phred scores for MNHN 8211 and 8212 were 48.6 and 57.3, respectively. Control region sequences for both individuals and the annotated mitogenome of MNHN 8211 assembled by Novoplasty were deposited in Genbank as OP994180, OP994181, and OP994173, respectively.

Genetic analyses

We used sequences retrieved from GenBank to generate two data sets: one comprising the mitochondrial control region (CR) of the two stranded specimens, 49 individuals representing various species of *Mesoplodon* (*M. bidens*, *M. densirostris*, *M. eueu*, *M. europaeus*, *M. ginkgodens*, *M. grayi*, *M. mirus*, and *M. stejnegeri*), and two northern bottlenose whales that acted as outgroup; and one comprising the entire mitogenomes of MNHN 8211 and 25 additional individuals representing *M. bidens*, *M. eueu*, *M. europaeus*, *M. ginkgodens*, and *M. mirus* (Supplemental Tables S1 and S2).

CR sequences were aligned in Clustal W 1.8 (Thompson *et al.*, 1994) and then subjected to phylogenetic analysis via Maximum Likelihood (ML) and Bayesian inference (BI). JModelTest v.2.1.17 (Darriba *et al.*, 2012) identified TPM3uf+I as the best-fitting nucleotide substitution model based on the Bayesian information

criterion (Schwarz, 1978). The ML analysis was carried out in PhyML 3.1 (Guindon and Gascuel, 2003) using NNI (fast-nearest neighbour interchange search) and 1000 bootstrap pseudoreplicates to estimate branch support. BI was implemented in MrBayes 3.2.7 (Ronquist et al., 2012) on the CIPRES Portal (Miller et al., 2010) and comprised two Markov chains in twelve separate runs of 20 million generations. Genetic differentiation between our specimens and other *Mesoplodon* spp. was assessed by computing pairwise *P*-distances in MEGA v. 11 (Kumar et al., 2018).

Divergence times were estimated based on the mitogenomes, including protein-coding genes (split by codon position), transfer and ribosomal RNA genes, and the D-loop region. Substitution models were determined via PartitionFinder2 (Lanfear et al., 2017) and subsets (Supplemental Table S3) linked with a relaxed clock log normal and a linked Yule tree model. We implemented three calibration points derived from the divergence dating analysis of Carroll et al. (2021), (Supplemental Table S4). The analysis was run in BEAST v.2.6.7 (Bouckaert et al., 2019) in three separate runs of 15 million generations, sampled every 10,000 generations. The results were then combined in Log Combiner (Bouckaert et al., 2019) after a 10% burn-in, convergence assessed via Tracer v1.7 (Rambaut et al., 2018), and a Maximum Clade Credibility summary tree calculated via TreeAnnotator (Bouckaert et al., 2019) with a burn-in of 20%. Finally, we estimated the mitochondrial nucleotide diversity (π) of individuals identified as *M. eueu* and *M. mirus* using DnaSP v.6 (Rozas et al., 2017).

Results and discussion

External appearance

Ramaris's and True's beaked whales cannot be consistently distinguished based on their external appearance (Carroll et al., 2021). Both share with our specimens the presence of a proportionally small head with a pronounced forehead bulge, a relatively short but distinct beak, a straight mouth line, and a single pair of teeth at the tip of the mandible (Supplementary Figure S1). As is normal in females (Moore, 1968), the teeth in MNHN 8211 and 8212 have not erupted.

The overall body colour of both species appears to be one of basic countershading (medium grey on top, lighter grey on the bottom), in addition to a dark patch around the eye and an area of whiter pigmentation that extends from the anus to the genital slit (Mead, 1989; Pitman, 2018; Carroll et al., 2021). The same pattern occurs in our stranded specimens, albeit less clearly so in MNHN 8212 owing to its advanced state of decomposition. In some individuals of *M. eueu* a pale area stretches from the dorsal fin back towards the flukes (MacLeod, 2018; Carroll et al., 2021). A similar patch can be seen in MNHN 8212 but not MNHN 8211 (Figure 4), suggesting ontogenetic variation in coloration patterns as observed in other ziphiids (Mead, 2009).

Skull morphometrics

The first two principal components of our PCA account for 83.8% of the variance and place our stranded individuals either side of the morphospace occupied by *M. eueu* (Table 1; Figure 5). Principal component 1 separates MNHN 8211 from all other specimens, with its shorter rostrum and mandibular symphysis likely reflecting its immature state. MNHN 8212 is located roughly halfway between the previously defined morphospace areas of *M. eueu* and *M. mirus*. Overall, these results are consistent with – though not conclusive proof of – both of our specimens representing *M. eueu*.



Figure 4. Caudal fins of both *Mesoplodon eueu* specimens stranded, dashed lines indicate the pale area over the peduncle that extends towards the flukes on MNHN 8212 (A) which is absent on MNHN 8211 (B).

Genetic analyses

The CR sequences of MNHN 8211 and 8212 are identical, suggesting that they are closely related. We hypothesize that they represent a mother-calf dyad, given that (i) one is an adult female and the other a calf/juvenile, (ii) both stranded within days of each other and in geographical proximity, and (iii) the more advanced decay of the adult (found three days later), which in turn suggests

Table 1. Cranial measurements taken in *Mesoplodon eueu* specimens stranded in Uruguay

	MNHN 8211	MNHN 8212
CBL	602.7	803.3
CH	247	330
RL	342.3	470.3
RW	174	204
PFW	110.3	118.3
PCW	137.3	159
BZW	274.7	343.7
ML	505.3	682.7
SL	99.7	185.3

CBL, Condylbasal length; CH, Cranial height; RL, Rostrum length; RW, Rostrum width between antorbital notches; PFW, Premaxillary sac fossa width; PCW, Width across preanarial crest; BZW, Bizygomatic width; ML, Mandible length; SL, Symphysis length. All measurements are in mm

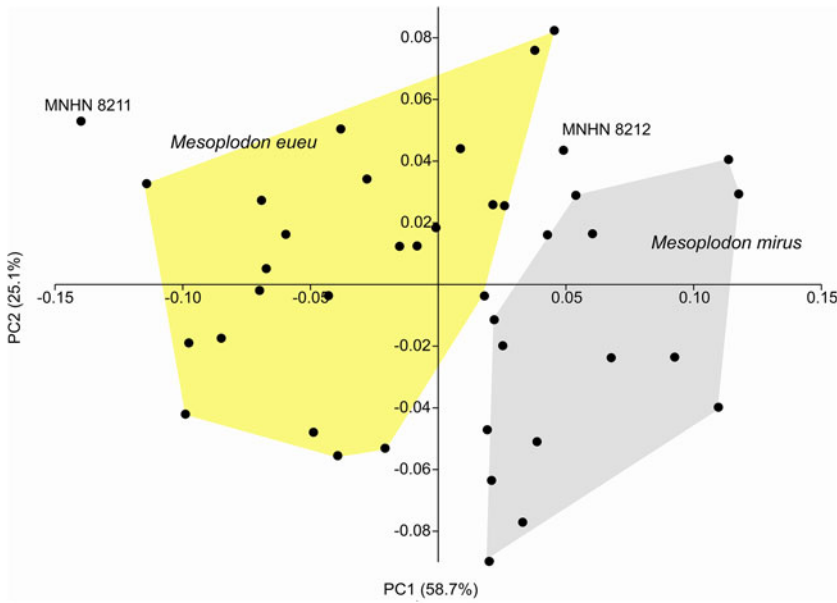


Figure 5. Principal component analysis of eight cranial and mandibular measurements shows that the two stranded Mesoplodon specimens from Uruguay (MNHN 8211 and 8212) plausibly cluster with *M. eueu*. Comparative data from Carroll *et al.* (2021).

that both may have died at a similar time. Alternatively, they could belong to the same population.

Breeding knowledge of beaked whales is scarce but the lactation period is thought to be of one to several years of duration (MacLeod, 2018). In some species it has been estimated to last from 3 to 5 years, and weaning occurs when the calf approximately doubles its size at birth (MacLeod and D’Amico, 2006; Feyrer *et al.*, 2020). The size at birth varies among species but offspring of some beaked whales range from 190 to 460 cm (Ferguson *et al.*, 2023), specifically for *M. mirus* a neonate of 220 cm of length has been reported (Ross, 1984). Taking this information into account and given the body length recorded on MNHN 8211, we suggest that this individual was still dependent on its mother.

Phylogenetic analysis of the CR data clusters our specimens with Ramari’s beaked whales and, consistent with our morphometric results, strongly supports their referral to *M. eueu* (Figure 6). The specimens thus correspond to the first confirmed record of this species from Uruguay and the Southwest Atlantic. Furthermore, it is probable that the previously reported stranding of True’s beaked whale from Southeastern Brazil (Souza *et al.*, 2005) may also represent *M. eueu*, given the currently known geographic distribution for *M. mirus* and *M. eueu* and that the latter was described after the stranding recorded in Brazil. This would imply an extension of the distribution range of *M. eueu* to the tropics.

As found previously (Carroll *et al.*, 2021), we recover *M. mirus* as sister to *M. eueu*. The *P*-distance between the Uruguayan

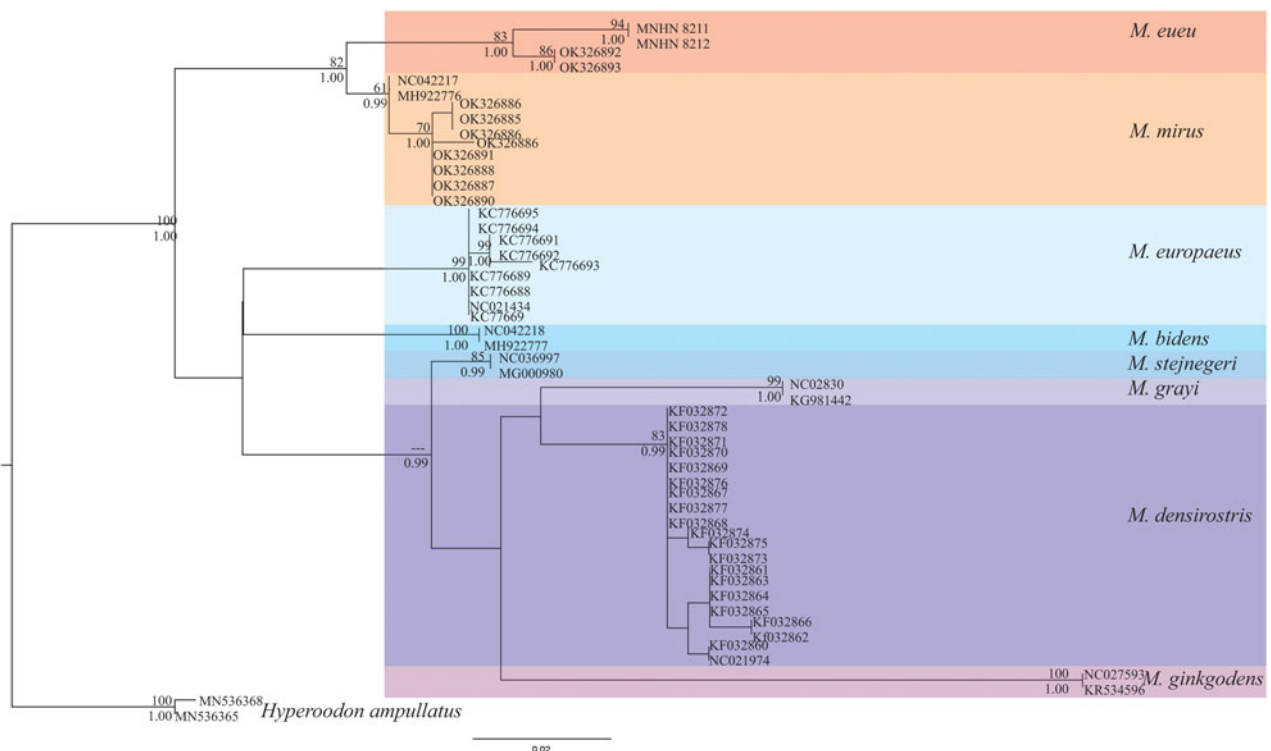


Figure 6. Bayesian phylogeny of Mesoplodon based on 51 mitochondrial control regions. Values above branches are ML bootstrap support, those below are Bayesian posterior probabilities.

individuals and other members of *M. eueu* is 0.0208 (variance = 0.0086), and that between the same specimens and *M. mirus* is 0.0432 (variance = 0.0105). Mitogenome analysis dates the last common ancestor of *M. eueu* to 0.8606 Ma (95% HPD: 0.118–1.7422 Ma) and the divergence of *M. eueu* from *M. mirus* to 2.5902 Ma (1.4201–3.9211 Ma; Supplementary Figure S2).

Our divergence time estimates somewhat predate those of Carroll *et al.* (2021) and reveal greater genetic diversity within Ramari's beaked whales than previously thought. This is reflected in the notable genetic distance between our individuals and previously analysed specimens of *M. eueu*. Specifically, we found a total of 164 substitutions between the mitochondrial genome of MNHN 8211 and the *M. eueu* sequences of Carroll *et al.* (2021), compared to 814 substitutions between *M. eueu* (including MNHN 8211) and *M. mirus*. With the inclusion of MNHN 8211, the mitochondrial nucleotide diversity of *M. eueu* now stands at 0.0070 (standard deviation = 0.0031). This is notably higher than in *M. mirus* (0.0024; SD = 0.0003), confirming the pattern previously described, and suggests a greater effective population size and/or possible population structuring, as seen in other ziphiids like bottlenose whales (Ellegren and Galtier, 2016).

Conclusion

We report the first confirmed record of Ramari's beaked whale from Uruguay and the wider Southwest Atlantic. Our findings expand the range and genetic diversity of this recently described species and suggest possible population structuring. Further samples from across the range of Ramari's beaked whale are needed to test this idea. Identifying a new species of marine mammal in Uruguayan waters calls for further resource allocation both to stranding responses and long-term systematic surveys of the regional coast.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315423000929>

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Author's contributions. LF, ER, PL, and MV collected the specimens analysed. NR and MV carried out the genetic and morphological analysis. ELC, MMcG, and FGM made substantial contributions to the conception of the work. All authors interpreted the data and discussed the results. All authors wrote and prepared the draft of the manuscript, and approved the final version of the manuscript.

Competing Interest. None.

Data Availability Statement. The data that support the findings of this study are openly available in GenBank at <https://www.ncbi.nlm.nih.gov/genbank/>, accession numbers are available in the manuscript text and Supplementary material S1.

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