

1 A new species of baleen whale (*Balaenoptera*) from the Gulf of Mexico, with a review of its  
2 geographic distribution

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21 **Abstract**

22  
23 Bryde’s-like whales are a complex of medium-sized baleen whales that occur in tropical waters  
24 of all three major ocean basins. Currently, a single species of Bryde’s whale, *Balaenoptera*  
25 *edeni* Anderson, 1879, is recognized, with two subspecies, Eden’s whale, *B. edeni edeni* and  
26 Bryde’s whale, *B. edeni brydei* (Olsen, 1913), although some authors have recognized these as  
27 separate species. Recently, a new, evolutionarily divergent lineage of Bryde’s-like whale was  
28 identified based on genetic data and was found to be restricted primarily to the northern Gulf of  
29 Mexico (GOMx). Here, we provide the first morphological examination of a complete skull  
30 from these whales and identify diagnostic characters that distinguish it from the other medium-  
31 sized baleen whale taxa. In addition, we have increased the number of genetic samples of these  
32 Bryde’s-like whales in the GOMx from 23 to 36 individuals, all of which matched the GOMx  
33 lineage. A review of Bryde’s-like whale records in the Caribbean and greater Atlantic supports  
34 an isolated distribution for this unique lineage, augmenting the genetic and morphological body  
35 of evidence supporting the existence of an undescribed species of *Balaenoptera* from the Gulf of  
36 Mexico.

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39 **KEYWORDS**

40 *Balaenoptera*, Bryde’s whale, cetacean, Gulf of Mexico, species description, systematics,  
41 taxonomy

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44 **1 | INTRODUCTION**

45

46 Despite being some of the largest animals on the planet and carrying the moniker of ‘charismatic  
47 megafauna’, it is always surprising to be reminded that the taxonomy and systematics of  
48 cetaceans, even today, remain in flux. Taylor et al. (2017b) surveyed the extant cetacean fauna  
49 and concluded that of the currently recognized taxa, 32% have a high likelihood of  
50 underclassification errors and that an accurate taxonomy may contain twice the number of  
51 subspecies currently recognized. For example, two subspecies of killer whales (*Orcinus orca*)  
52 are currently recognized, but recent studies have suggested there are additional unrecognized  
53 subspecies or even species (Leduc et al., 2008). Taylor et al. (2017b) concluded that the primary  
54 problems encountered when trying to address questions in cetacean taxonomy include the  
55 difficulty of obtaining skulls or obtaining tissue samples from elusive, often remote and difficult  
56 to sample taxa, coupled with the legal protections they are given. Due to these problems, studies  
57 often have inadequate numbers of samples, and/or an inadequate geographic sampling of these  
58 typically widely distributed species. As a result, robust taxonomic inference is often severely  
59 hindered.

60

61 Members of the “Bryde’s whale complex” in the genus *Balaenoptera* provide an excellent  
62 example of the historical and contemporary confusion that exists in cetacean taxonomy. These  
63 tropical and subtropical, and generally nonmigratory whales, are found in all major ocean basins.  
64 They are difficult to distinguish visually based on external morphology and are therefore often  
65 collectively referred to as the “Bryde’s whale complex” or “Bryde’s-like whales.” Currently a  
66 single species of Bryde’s whale, *Balaenoptera edeni* Anderson, 1879, is recognized, with two  
67 recognized subspecies, Eden’s whale, *B. edeni edeni* and Bryde’s whale, *B. edeni brydei* (Olsen,

68 1913) (Committee on Taxonomy, 2019). These two subspecies have previously also been  
69 considered species based on morphological data (Soot-Ryen, 1961; Wada et al., 2003) and  
70 supported by genetic data (Rosel & Wilcox, 2014; Wada et al., 2003); see Rice (1998) for a  
71 historical review of differing opinions on the taxonomy of these whales. Genetic analysis of the  
72 type specimen for *B. edeni* has not yet been completed and a type specimen was not designated  
73 for *B. brydei* when it was named. As a result, despite the multiple lines of evidence for species-  
74 level differences, there has been a conservative treatment of the taxonomic rank of these two  
75 members and they are both currently recognized as subspecies of *B. edeni* (Committee on  
76 Taxonomy, 2019).

77  
78 *Balaenoptera edeni* Anderson, 1879 was first described from a medium-sized balaenopterid  
79 whale that stranded in Myanmar in 1871 (Anderson, 1878 [1879]). They are thought to inhabit  
80 coastal waters of the Indian Ocean and the western Pacific, with genetically confirmed records  
81 from the East and South China seas and coastal waters throughout the northern Indian Ocean  
82 from Oman east to Indonesia (Jayasankar et al., 2009; Kershaw et al., 2013; Kim et al., 2018; Li  
83 et al., 2019; Rosel & Wilcox, 2014; Sasaki et al., 2006; Wada et al., 2003; Yoshida & Kato,  
84 1999; Yusmalinda et al., 2017). To date there are no records from the Atlantic basin or the  
85 eastern Pacific. *B. brydei* Olsen, 1913 was described based on whales taken by the whaling  
86 industry in Saldanha Bay, South Africa (Olsen, 1913). These whales are generally associated  
87 with deeper, more pelagic waters and have a much broader worldwide distribution, with  
88 genetically confirmed records from the Atlantic, Pacific, and Indian Ocean basins (Alves et al.,  
89 2010; Herath, 2007; Kanda et al., 2007; Kershaw et al., 2013; Kim et al., 2018; Luksenburg et

90 al., 2015; Murakami et al., 2018; Pastene et al., 2015; Penry, 2010; Penry et al., 2018; Rosel &  
91 Wilcox, 2014; Sasaki et al., 2006; Wada et al., 2003; Yoshida & Kato, 1999).

92

93 As recently as 2003, a new species of Bryde's-like whale was removed from the complex when  
94 Wada et al. (2003) described a smaller balaenopterid, Omura's whale, *Balaenoptera omurai*.

95 The authors suggested, based on morphological comparisons of the skull, that *B. omurai* and the  
96 two *B. edeni* subspecies each have diagnostic features in the morphology of the vertex of the  
97 skull, and that all three should be considered distinct species: *B. omurai*, *B. edeni*, and *B. brydei*.

98 Genetic analyses based on mitochondrial DNA (mtDNA) control region sequence data were  
99 consistent with the morphological distinctiveness of all three taxa, returning well-supported,

100 reciprocally monophyletic groupings of the currently recognized *B. omurai*, *B. e. edeni*, and *B. e.*

101 *brydei* (Kershaw et al., 2013; Rosel & Wilcox, 2014; Sasaki et al., 2006). Interestingly, while

102 originally thought to be restricted to the western Pacific and the tropical eastern Indian oceans

103 (Cerchio et al., 2019; Yamada, 2009), Omura's whales have now been recorded from the western

104 and central Indian Ocean (Cerchio et al., 2015; Cerchio et al., 2019), and from the eastern and

105 western tropical Atlantic Ocean, near and south of the equator (Cypriano-Souza et al., 2017;

106 Jung et al., 2016), indicating that the confusion in distinguishing amongst members of this

107 closely related group of whales in the field has dramatically impaired understanding of each

108 member's taxonomy, genetics, and distribution. Cerchio et al. (2019) provide a comprehensive

109 review of the distribution of this species.

110

111 Most recently, Rosel and Wilcox (2014) identified a new, evolutionarily distinct lineage of

112 Bryde's-like whales in the Gulf of Mexico (GOMx) (Fig. 1). The presence of Bryde's whales in

113 the GOMx was first recognized in 1965 (Rice, 1965) based on a whale that stranded alive on  
114 April 2, 1965 in the panhandle of Florida and was later towed to sea. Historically, these whales  
115 were assumed to be a population of the broadly distributed *B. edeni* species. Analysis of  
116 mitochondrial DNA (mtDNA) control region sequences of whales sampled in the northeastern  
117 GOMx revealed that this population is evolutionarily distinct from all other whales within the  
118 Bryde's whale complex and all other known balaenopterid species (Rosel & Wilcox, 2014).  
119 Phylogenetic analyses placed these GOMx whales on a strongly supported lineage separated  
120 from *B. e. edeni* and *B. e. brydei* sampled in the Atlantic, Pacific, and Indian Oceans (Rosel &  
121 Wilcox, 2014). Within the first 375 base pairs of the mtDNA control region, the whales from the  
122 GOMx exhibited 25 fixed differences differentiating them from *B. e. edeni* and *B. e. brydei*  
123 (Rosel & Wilcox, 2014). This number of fixed differences is two to three times greater than that  
124 observed between recognized right whale species (*Eubalaena* spp.) and is of the same magnitude  
125 as the number of fixed differences found between fin (*B. physalus*) and blue (*B. musculus*)  
126 whales over the same gene region (Rosel et al., 2017). For further comparison, Archer et al.  
127 (2013) found only two fixed differences between the fin whale subspecies in the North Atlantic  
128 and North Pacific.

129

130 Rosel and Wilcox (2014) recommended that, based on the significant number of diagnostic  
131 differences and the finding of reciprocal monophyly, the whales in the GOMx should be given  
132 taxonomic status equivalent to the currently recognized subspecies, but they did not provide a  
133 species description. This omission was due largely to the lack of an intact specimen to represent  
134 the holotype for the new taxon. In addition, criteria for recognizing species and subspecies of  
135 cetaceans based on mtDNA sequence data were also lacking at the time.

136

137 In January 2019, an adult male Bryde's-like whale stranded and died in the Everglades on the  
138 southwestern coast of Florida in the GOMx (field number FMMSN1908). The entire specimen  
139 was collected and the intact skull and skeleton were deposited into the Smithsonian National  
140 Museum of Natural History collection (USNM 594665). In addition, Taylor et al. (2017a)  
141 described new guidelines and thresholds for delimiting cetacean subspecies and species using  
142 mtDNA control region sequence data. Here we re-examine the genetic distinctiveness of the  
143 Bryde's-like whales in the GOMx, adding data from new samples collected since the initial  
144 publication of Rosel and Wilcox (2014), new DNA sequence data available from recent  
145 publications on Bryde's whales worldwide, and in light of the guidelines and thresholds provided  
146 in Taylor et al. (2017a). We also provide a description of the morphological characteristics of  
147 the new specimen. The joint genetic and morphological data provide strong support for a new  
148 species of *Balaenoptera*.

149

## 150 **2 | METHODS**

### 151 **2.1 | Genetic data**

152 Rosel and Wilcox (2014) sequenced the complete mtDNA control region from 18 Bryde's-like  
153 whales remotely biopsied in the northeastern Gulf of Mexico (GOMx), three whales that  
154 stranded in the GOMx and two that stranded on the U.S. east coast. Here we add new DNA  
155 sequence data from 18 new skin samples collected between 2012 and 2019: 14 biopsy samples  
156 collected in the northeastern GOMx, the first biopsy sample ever collected in the western GOMx  
157 off Texas, and skin collected from two whales that stranded in Louisiana and a whale that

158 stranded in Flamingo, Florida Bay, Everglades National Park. DNA was extracted using a  
159 standard proteinase K digestion followed by organic extraction (Rosel & Block, 1996) or a  
160 Qiagen DNeasy Blood and Tissue Kit following the manufacturer's instructions. DNA quality  
161 and quantity were assessed through gel electrophoresis and fluorometry, respectively. The  
162 complete mtDNA control region was amplified and sequenced in two overlapping fragments and  
163 the sex of each biopsy was genetically determined as described in Rosel and Wilcox (2014).  
164 Control region PCR products were purified via low melting point agarose gel extraction followed  
165 by agarose digestion or purified enzymatically using Exonuclease I and FastAP Thermosensitive  
166 Alkaline Phosphatase (Thermo Scientific). All PCR products were sequenced in both directions  
167 using the Applied Biosystems BigDye Terminator v1.1 cycle sequencing kit and run on an ABI  
168 3130 or ABI 3500 Genetic Analyzer or sequenced commercially using a BigDye Terminator  
169 v3.1 cycle sequencing kit (Eurofins MWG Operon) on an ABI 3730xl Genetic Analyzer.  
170 Forward and reverse reads were independently edited using Sequencher v5.4.6 (GeneCodes) or  
171 Geneious Prime 2020.0.5 (<https://www.geneious.com>) and a final consensus sequence for each  
172 sample was assembled.

173

174 In an effort to locate a specimen that could serve as a holotype, we found a specimen at the  
175 Louisiana State University Museum of Natural History (LSUMZ 17027) that had been collected  
176 in 1954 and identified as a possible Bryde's whale (Lowery, 1974). In order to verify the  
177 species, we extracted and sequenced DNA from the specimen. A section of one occipital  
178 condyle was cleaned with 5% bleach solution and rinsed with distilled water, and surface bone  
179 removed by drilling with a sterile 3 mm drill bit. The drill bit was exchanged for a new sterile  
180 bit and bone powder then collected from within the condyle bone. DNA extraction was



181 performed in an ancient DNA only laboratory where all surfaces and laboratory equipment were  
182 cleaned with 10% bleach prior to performing the extraction. DNA was extracted from 50 mg of  
183 bone powder using the Qiagen QIAamp DNA Investigator Kit after demineralization of the  
184 powder in 950  $\mu$ l of 0.5 M EDTA (pH 8.0) at room temperature for 18 hr. Extraction was  
185 performed according to the manufacturer's protocol for isolation of DNA from bone with the  
186 following adjustments: Buffer ATL was decreased from 360  $\mu$ l to 330  $\mu$ l, Buffer AL with carrier  
187 RNA was increased from 300  $\mu$ l to 700  $\mu$ l, and the ethanol added prior to binding to the QIAamp  
188 MinElute column was increased from 150  $\mu$ l to 350  $\mu$ l. A negative DNA extraction control was  
189 simultaneously run using 950  $\mu$ l of 0.5 M EDTA (pH 8.0).

190

191 For this bone sample, the 5' end of the mtDNA control region was amplified and sequenced  
192 using five overlapping fragments ranging from 132 to 160 base pair (bp) in length. The  
193 following sets of primer pairs were used to obtain control region sequence: L15874 (Vollmer et  
194 al., 2011) and Bede143R (5'-ATTAATTAAGTTATAGGAAGGT-3') annealing temperature  $T_a$   
195 = 50°C; Bede121F (5'-CTTGTCTTATCACATATTATT-3') and Bede229R (5'-  
196 CTTCAACTGCTCGTGGT-3')  $T_a$  = 50°C; Bede218F (5'-TGCTATGTATAACTGTGCATTC-  
197 3') and Bede310R (5'-GACTGGGGAATGCATAACAG-3')  $T_a$  = 45°C; BedeShort145F (5'-  
198 ACCACGAGCAGTTGAAGTCC-3') and BedeShort145R (5'-  
199 TCGTGATCTAATGGAGCGGC-3')  $T_a$  = 55°C; BedeShort89F (5'-  
200 TGCTGTTATGCATTCCCCAGT-3') and H16265 (Rosel et al., 1999)  $T_a$  = 50°C. Each PCR  
201 was performed in a 50  $\mu$ l reaction with 20 mM Tris-HCl (pH 8.4), 50 mM KCl, 1.5 mM MgCl<sub>2</sub>,  
202 150  $\mu$ M dNTPs, 2.5 U *Taq* DNA Polymerase (Invitrogen), 0.12 mg/ml BSA, 0.3  $\mu$ M of each  
203 primer and 4 – 5  $\mu$ l of DNA. The PCR profile included an initial denaturation step of 95°C for

204 30 s followed by 45 cycles of 95°C for 30 s, T<sub>a</sub> as listed above for 30 s, and 72°C for 30 s with a  
205 final extension at 72°C for 7 min. PCR products were purified using Exonuclease I and FastAP  
206 Thermosensitive Alkaline Phosphatase (Thermo Scientific) and sequenced in both directions  
207 using the Applied Biosystems BigDye Terminator v1.1 cycle sequencing kit on an ABI 3130  
208 Genetic Analyzer. Forward and reverse reads were independently edited using Geneious Prime  
209 2020.0.5 and consensus sequences for each fragment were created then assembled to create one  
210 continuous sequence of the 5' end of the control region. The final sequence was compared to the  
211 control region haplotypes of baleen whales recovered in the GOMx and western North Atlantic.

212

213 The Bayesian phylogenetic analysis presented in Rosel and Wilcox (2014) was repeated with the  
214 addition of the new sequences described above and augmented with new sequences from the  
215 other Bryde's whale taxa published since 2014 and available in GenBank. The additional  
216 published sequences expanded the geographic range of the original phylogenetic analysis to  
217 include localities of Bryde's whales, *B. e. brydei*, in the southern Caribbean (Luksenburg et al.,  
218 2015), the East China Sea (Kim et al., 2018), the California coast of the eastern North Pacific<sup>1</sup>,  
219 off the coast of Chile in the eastern South Pacific (Pastene et al., 2015) and the coast of Brazil in  
220 the western South Atlantic (Pastene et al., 2015). The geographic range of Eden's whale, *B. e.*  
221 *edeni*, was increased by including new sequences from stranded whales in Bali, Indonesia in the  
222 eastern Indian Ocean (Yusmalinda et al., 2017) and the South China Sea (Li et al., 2019).  
223 Because the published sequences available in GenBank are of varying lengths, we performed the  
224 phylogenetic analysis on three different control region alignments: a 305 bp alignment that

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<sup>1</sup> Unpublished data. M. E. Flannery and A. B. Sellas. Ornithology and Mammalogy, California Academy of Sciences, 55 Music Concourse Drive, San Francisco. GenBank accession number KY938508.

225 allowed us to include the broadest geographic coverage of the Bryde's whale complex contained  
226 73 haplotypes, a 375 bp alignment containing 22 haplotypes and finally a 721 bp alignment  
227 containing 11 haplotypes. The latter alignment still allowed for coverage of all members of the  
228 Bryde's whale complex and geographic coverage from the North Atlantic (including the GOMx  
229 and Caribbean Sea), South Atlantic, North Pacific (including the East and South China Seas),  
230 and the South Pacific. The alignments also included haplotypes from *B. omurai* and from other  
231 balaenopterid whales, while *Eubalaena glacialis* served as the outgroup (Table S1). All  
232 sequences were aligned using MUSCLE v3.8.425 and default parameters in Geneious Prime  
233 2020.0.5.

234

235 Phylogenetic analyses were performed on each alignment using MrBayes v3.2.6 (Huelsenbeck &  
236 Ronquist, 2001). First, jModeltest v2.1.6 (Posada, 2008) and the Bayesian information criterion  
237 (BIC) were used to determine the best model given the control region alignments; TPMuf+G for  
238 the 305 and 375 bp alignments and TPM3uf+I+G for the 721 bp alignment. As a result, the  
239 more parameterized general time reversible (GTR) model with appropriate corrections (gamma  
240 and/or invariable sites) was used. For each alignment, MrBayes was run in Geneious Prime  
241 2020.0.5. Bayesian searches used 4 chains, 2 runs, and 5,000,000 generations using default  
242 priors in MrBayes. Burn-in was set to 25%. Convergence of the runs was determined by  
243 examining the average standard deviation of split frequencies and using Tracer v1.5 (Rambaut &  
244 Drummond, 2007).

245

246 A characteristic attributes (CAs) diagnosis (Davis & Nixon, 1992; Lowenstein et al., 2009;  
247 Sarkar et al., 2002) was performed using the control region sequences of *B. e. edeni*, *B. e. brydei*,

248 *B. omurai*, and the haplotypes from the GOMx whales for the 305 bp control region alignment  
249 using all sequences available in GenBank. While it is the shortest alignment, the 305 bp region  
250 allows us to include the greatest number of haplotypes for all taxa involved, thereby improving  
251 the likelihood that identified diagnostic sites are reflect true interspecific differences and not  
252 simply intraspecific variability.

253

254 Subsequent to the identification of this unique lineage of whales in the GOMx in 2014, standards  
255 and guidelines for delimiting cetacean species and subspecies based on mtDNA control region  
256 sequences were established by Taylor et al. (2017a). Rosel et al. (2017) surveyed levels of  
257 genetic divergence in the mtDNA control region between accepted pairs of species, subspecies,  
258 and populations of cetaceans, and explored the efficacy of different metrics of genetic divergence  
259 for correctly identifying these different taxonomic levels. They found that the genetic measure  
260 of net nucleotide divergence or  $d_A$  (Nei, 1987) performed well at distinguishing species from  
261 subspecies and populations. This metric provides a measure of number of net nucleotide  
262 substitutions or net divergence between two groups, accounting for the level of within group  
263 variability. Taylor et al. (2017a) built on these results, recommending quantitative standards for  
264 delimiting new species and subspecies based on  $d_A$  coupled with a measure of diagnosability  
265 (defined as “a measure of the ability to correctly determine the taxon of a specimen of unknown  
266 origin based on a set of distinguishing characteristics” (Archer et al., 2017)). If  $d_A > 0.02$   
267 between two groups of cetaceans, those groups exceed the threshold of net nucleotide divergence  
268 consistent with species level differences and could warrant species status when also coupled with  
269 a diagnosability of at or near 100%. In cases where  $0.004 < d_A < 0.02$  between two taxonomic

270 groups, those groups exhibit levels of genetic divergence consistent with subspecies. To place  
271 the degree of divergence of the Bryde's-like whales from the GOMx into this context, we  
272 estimated net nucleotide divergence,  $d_A$  (Nei, 1987), for both Bryde's whale subspecies,  
273 Omura's whale and sei whale, *B. borealis*, sequences of the 375 bp alignment using MEGA X:  
274 Molecular Evolutionary Genetics Analysis across computing platforms (Kumar et al., 2018;  
275 Stecher et al., 2020). For one haplotype, information on the number of individuals with the  
276 haplotype was not provided in the publication and was therefore assigned as a single individual.  
277 Fixed differences were calculated using DNAsp v6.12.03 and fixed indels determined by  
278 viewing the alignments in Geneious Prime 2020.0.5.

279

280 All of the new samples except for the bone sample (LSUMZ 17027) were genotyped at the 17  
281 microsatellite loci identified as polymorphic in Rosel and Wilcox (2014) using a Qiagen Type-it  
282 Microsatellite PCR kit and the manufacturer's protocols. The loci used were: GATA028,  
283 GATA053, GATA098, GATA417, GGAA520 (Palsbøll et al., 1997), AC137, CA234, GT023,  
284 GT122, GT307, GT541 (Bérubé et al., 2005), EV104 (Valsecchi & Amos), Ppho130, Ppho137  
285 (Rosel et al., 1999), SW13 (Richard et al., 1996), GM199/200, GM417/418 (Amos et al., 1993).  
286 Reverse primers for all loci except GATA028, GATA053, GT023 and Ppho137 were pigtailed  
287 following Brownstein et al. (1996). Multiplexing allowed all 17 loci to be genotyped in three  
288 PCR reactions (Table S2). All PCR reactions included positive and negative no-DNA controls.  
289 Resultant PCR products, including all controls, were genotyped on an ABI 3130 or an ABI 3500  
290 Genetic Analyzer using Genescan 500 LIZ or Genescan 600 LIZ v2.0 dye size standard (Applied  
291 Biosystems), respectively. The raw data were scored using GeneMapper v6 (Life  
292 Technologies/Applied Biosystems). Observed and expected heterozygosities and the number of

293 alleles per locus were calculated using Arlequin v3.5 (Excoffier & Lischer). In order to identify  
294 whether multiple biopsies were collected from the same animals, we used Microsatellite Toolkit  
295 (Park, 2001) to search for individuals with identical multilocus genotypes and we estimated  
296 probability of identity  $P_{(ID)}$  and the more conservative  $P_{(ID)sib}$  (Waits et al., 2001) using  
297 GenAlEx v6.5 (Peakall & Smouse, 2006). Samples identified as having identical genotypes  
298 were also checked to see that they had the same sex and the same control region sequence.

299

## 300 **2.2 | Morphological data**

301 On 29 January 2019, a 1,126 cm adult male Bryde's-like whale (FMMSN1908) stranded in  
302 Flamingo, Florida Bay, Everglades National Park, on the southwestern coast of the Florida  
303 Peninsula in the GOMx. The Florida Fish and Wildlife Conservation Commission (FWC)-  
304 Southwest Field Laboratory coordinated with NOAA National Marine Fisheries Service,  
305 Southeast Fisheries Science Center and volunteers from multiple agencies to salvage the carcass  
306 for full necropsy and preservation. A suite of external observations was taken by the stranding  
307 responders and the carcass was then buried in Fort De Soto Park, Florida. In October 2019, after  
308 being moved from Florida to North Carolina for further cleaning, the entire skeleton was  
309 exhumed, cleaned further and deposited in the U.S. Museum of Natural History at the  
310 Smithsonian Institution (USNM 594665). We took ten measurements of the skull (Table 1) to  
311 the closest millimeter using a calipers and photographed the skull. In addition, we examined and  
312 compared the characteristics of the vertex of the skull identified by Wada et al. (2003) as  
313 important for distinguishing among the different Bryde's whale taxa, including Omura's whale.  
314 These include the shape and extent of the ascending process of the posterior end of the maxilla,  
315 the extent to which the frontals are exposed, the extension of the premaxilla and whether it

316 reaches the frontal, and whether the alisphenoid and squamosal bones are in contact. We also  
317 directly compared these features between this whale (USNM 594665) and USNM 572922, a  
318 subadult male that stranded on the North Carolina coast in 2003 that has been genetically  
319 confirmed to belong to the lineage that identifies the Bryde’s-like whales in the GOMx (Rosel &  
320 Wilcox, 2014).

321

### 322 **2.3 | Distributional data**

323 The National Marine Fisheries Service (NMFS), Southeast Fisheries Science Center (SEFSC)  
324 has conducted marine mammal vessel and aerial surveys in the northern GOMx, covering  
325 nearshore, continental shelf and slope, and oceanic waters out to the U.S. EEZ since the late  
326 1980s. We reviewed and compiled all “Bryde’s whale”, “*Balaenoptera* sp.” and “Bryde’s/sei  
327 whale” sightings from these GOMx surveys spanning 1989–2019. We similarly compiled and  
328 reviewed all NMFS marine mammal vessel and aerial surveys in the U.S. EEZ of the Atlantic  
329 coast between 1992 and 2019. Depths at each visual sighting location were extracted using  
330 ArcGIS and the ETOPO2 2-arc-minute gridded global relief dataset.

331

332 We also reviewed 13 sightings records provided by the Bureau of Ocean Energy Management  
333 (BOEM) made by protected species observers (PSO) on seismic vessels in the GOMx from  
334 2010–2014 as part of the required mitigation measures. These observers record time, location,  
335 distance to vessel, water depth, species, a visual description of the whale and additional sighting  
336 details for each sighting. As other whales are present in the GOMx, including sperm whales and  
337 beaked whales (Family Ziphiidae), which, at a distance, could potentially be confused with a

338 baleen whale, we evaluated each sighting description to determine the likelihood the sighting  
339 was of a Bryde's-like whale.

340

341 Finally, we reviewed stranding data from the U.S. GOMx coast and the U.S. Atlantic seaboard  
342 for those strandings listed as "Bryde's whales" through query of the NOAA National Marine  
343 Mammal Health and Stranding Response Database and the Division of Mammals Collections at  
344 the Smithsonian National Museum of Natural History (USNM), including examination of all  
345 written records in the USNM archive. While stranding data can potentially provide some  
346 information on cetacean distribution, it is important to recognize that stranding location may not  
347 always represent habitat or area of origin due to currents and winds moving carcasses away from  
348 normal distribution. We also reviewed the published literature for both regions and also  
349 broadened the search to cover the entire Atlantic Ocean to further evaluate the distribution of  
350 Bryde's whale taxa in the Atlantic Basin.

351

352

### 353 **3 | Results**

#### 354 **3.1 | Genetic data**

355 The full mtDNA control region (936 bp) was successfully sequenced for 15 new remote skin  
356 biopsy samples and three strandings. No new haplotypes were found; all new animals exhibited  
357 the most common haplotype (Bede001, GenBank accession KJ586818). The 5' end of the  
358 mtDNA control region (381 bp) that was sequenced for bone sample LSUMZ 17027 also  
359 matched the Bede001 haplotype. In combination with those samples presented in Rosel and



360 Wilcox (2014), a total of 42 whale tissue samples (35 biopsies, 7 strandings) have been analyzed  
361 from the GOMx and two strandings from the Atlantic.

362

363 All tissue samples were successfully genotyped at the 17 microsatellite loci. Only a single new  
364 allele was found at locus GATA098, despite increasing the overall genotyped sample size by 59  
365 %. Probabilities of identity ( $P_{ID} = 1.50 \times 10^{-4}$ ;  $P_{ID(sib)} = 1.36 \times 10^{-2}$ ) were relatively high due to  
366 the low heterozygosity exhibited by all the loci (Table S2). Microsatellite Toolkit identified 8  
367 duplicate samples across the pooled old and new sample set, with several animals biopsied eight  
368 to nine years apart. After removing duplicate samples, and including the LSU specimen, the  
369 total number of individual whales sampled in the northern GOMx and the two strandings on the  
370 east coast between 1954 and 2019 is 36. The sex ratio across these unique individuals (biopsies  
371 and strandings) is 19F:15M; the sex of two stranded animals could not be determined.

372

373 The Bayesian analyses based on the mtDNA control region alignments revealed the same pattern  
374 found previously (Rosel & Wilcox, 2014). *B. e. edeni*, *B. e. brydei*, and the Bryde's-like whales  
375 in the GOMx are each reciprocally monophyletic with posterior probabilities of 0.99 to 1.0 (Fig.  
376 2, Figures S1, S2). The characteristic attributes diagnosis on the 305 bp control region alignment  
377 identified a total of 30 diagnostic sites that distinguish among *B. e. brydei*, *B. e. edeni*, *B. omurai*,  
378 and the Bryde's-like whales from the GOMx (Table 2). These include 24 of the 25 diagnostic  
379 sites reported in Rosel and Wilcox (2014) and five additional sites previously described in  
380 Cypriano-Souza et al. (2017). Nucleotide position 15682 was counted in error in Rosel and  
381 Wilcox (2014) as a diagnostic position. A novel diagnostic site for the Bryde's-like whales from

382 the GOMx not previously noted (position 15564) was identified due to removal of one *B. e.*  
383 *brydei* haplotype (GenBank accession EF068039) due to sequencing error reported by the  
384 authors<sup>2</sup>. The total number of diagnostic positions for each of the four taxa was: *B. e. edeni* (n =  
385 2), *B. e. brydei* (n = 3), *B. omurai* (n = 16), and Bryde's-like whales from the GOMx (n = 10).  
386 Nei's net nucleotide divergence,  $d_A$ , between the whales from the GOMx and the two *B. edeni*  
387 subspecies based on the 375 bp alignment ranged from 0.103 to 0.128 (Table 3), significantly  
388 greater than the minimum value of 0.02 for species level distinction identified by Taylor et al.  
389 (2017a). The number of fixed differences likewise remains high between the whales from the  
390 GOMx and those elsewhere (Table 3) and provide 100% diagnosability based on this gene  
391 region.

392

### 393 **3.2 | Morphological data**

394 The whale that stranded in January 2019 was an adult male (Fig. 3). Total length was 1,126 cm.  
395 The whale was a uniform dark gray on the dorsal side with a large falcate dorsal fin; the flippers  
396 were uniformly dark. The ventral side was lighter in coloration, particularly on the ventral side  
397 of the peduncle. The ventral side of the tail was lighter in color, particularly towards the middle  
398 and at the peduncle. Three ventral pleats extended past the umbilicus at the midline. The pleats  
399 were counted from the right lateral aspect to the mid-line; in line with the flipper insertion, 27  
400 pleats were counted, given a total count of 54 pleats. As is typical for all Bryde's-like whales,  
401 three ridges were present on the rostrum.

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<sup>2</sup> L. Pastene, pers comm. Institute of Cetacean Research, Tokyo, Japan. February 2020

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Wada et al. (2003), Yamada et al. (2006), and Yamada et al. (2008) utilized several diagnostic characteristics of the skull to distinguish between *B. e. edeni*, *B. e. brydei*, and *B. omurai*. Omura's whales exhibit the most differences, including two foramina on the parieto-squamosal suture. *B. e. edeni* is unique in the shape of the ascending process of the maxilla (slender and round) and in the broadly exposed frontal bones and the 'pedestal' they form for the ascending process of the maxilla (Wada et al., 2003). We utilized the diagnostic characters indicated by Wada et al. (2003), Yamada et al. (2006); Yamada et al. (2008) to examine the skull of the 2019 stranded whale (USNM 594665). The foramina seen in Omura's whale were not present in the 2019 stranded whale (USNM 594665). The Bryde's-like whales from the GOMx are further distinguished from *B. omurai* by the posterior end of the premaxillae, which reach the frontals in the GOMx whales but not in *B. omurai*. In the GOMx whales, the frontals are only narrowly exposed, forming a thin, narrow belt, clearly distinguishing them from *B. e. edeni*. In these characteristics of the vertex of the skull, the GOMx whales are most similar to *B. e. brydei*. However, we identified several characteristics in the vertex consistent in both the 2019 specimen (USNM 594665) and the immature whale specimen collected in North Carolina (USNM 572922) that are unique to the Bryde's-like whales from the GOMx and can be used to separate them from the other Bryde's whale subspecies and from *B. omurai*. We observed that the anterior portion of the frontal bones wraps around the posterior end of the nasals and protrudes on their medial side to separate the posterior end of the nasals. In addition, the posterior end of the nasals curves laterally and has relatively smooth margins, while in *B. e. brydei* the posterior end of the nasals remains straight and has somewhat crenulated margins.

425 **3.3 | Distributional data**

426 3.3.1 Gulf of Mexico

427 Compilation of 181 visual sightings from NMFS marine mammal aerial and vessel surveys  
428 between 1989 and 2019 indicates these whales currently have a restricted distribution along the  
429 continental shelf break near the De Soto Canyon area of the northeastern GOMx (Fig. 4). The  
430 water depths of visual sightings ranged from 117 m to 408 m with all but two in the range of  
431 151–352 m. In addition, a whale tagged in this area in October 2010 was satellite-tracked for a  
432 month, during which time the animal remained in waters between 100 and 400 m depth within  
433 the northeastern GOMx (Soldevilla et al., 2017).

434

435 During this survey period (1989–2019), two of the 181 sightings were of a large baleen whale  
436 (recorded as *Balaenoptera* sp. or Bryde’s/sei whale) in the western GOMx west of the  
437 Mississippi River delta in waters less than 300 m deep, but neither could be identified to species.  
438 However, in August 2017, the first confirmed sighting of a live Bryde’s-like whale in the  
439 western GOMx was made during a NMFS vessel survey (National Marine Fisheries Service,  
440 2018). This whale was seen off the Texas coast in 225 m water depth. Analysis of the mtDNA  
441 control region from a skin biopsy sample collected from the whale confirmed that it belongs to  
442 the lineage unique to Bryde’s-like whales from the GOMx. Finally, acoustic moorings placed in  
443 the western GOMx south of Louisiana have recorded some unique vocalizations thought to  
444 belong to Bryde’s-like whales from the GOMx<sup>3</sup>. Both the recordings and the sighting in the

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<sup>3</sup> M. Soldevilla, pers comm. NMFS Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, Florida, 33149. July 2019.

445 western GOMx were in water depths similar to the habitat used by the whales in the northeastern  
446 GOMx.

447

448 Examination of 13 sightings provided by BOEM from marine mammal observers on seismic  
449 vessels provided only minimal insight. No sightings were close enough for observers to record  
450 whether the diagnostic lateral ridges on the dorsal surface of the head were visible and thus none  
451 could unequivocally be identified as a Bryde's-like whale. Five sightings were in water depths  
452 >1,000 m, which is inconsistent with the Bryde's-like whales in the GOMx, and several of these  
453 observations described surfacing followed by multiple blows, a behavior more consistent with  
454 sperm whales recovering after a deep dive. These five sightings were ruled out as likely baleen  
455 whale sightings. Two sightings were within the known habitat in the northeastern GOMx, in  
456 waters of an appropriate depth suggesting they were likely Bryde's-like whales. Two sightings  
457 had useful photographs indicating a baleen whale with a distinctive falcate dorsal fin and were  
458 likely either a Bryde's whale or a stray sei whale. The four remaining sightings were in depths  
459 consistent with Bryde's whales, and several of these had descriptions of behavior consistent with  
460 them as well, e.g., two or more vertical blows before diving. These four sightings could not be  
461 ruled out based on the available information. While significant uncertainty remains with respect  
462 to the identity of whales sighted by PSO observers, four of the sightings were made along the  
463 continental shelf break west of the Mississippi River Delta (Fig. 4).

464

### 465 3.3.2 Atlantic Ocean

466 There are no confirmed at-sea sightings of any type of Bryde's whale along the U.S. eastern  
467 seaboard during NMFS marine mammal vessel and aerial surveys between 1992 and 2019,

468 despite considerable survey effort in the U.S. EEZ from Florida through Maine (~854,721 km of  
469 on-effort track line surveyed). There were five ship-based and one aerial survey-based sightings  
470 recorded as “Bryde’s/sei whales” from the early 1990s (Fig. 4). None of these sightings were  
471 close enough to identify rostral ridges and five were in waters greater than 1,000 m suggesting  
472 they were either the pelagic form of Bryde’s whale (*B. e. brydei*) or were sei whales. The  
473 southernmost sighting of a Bryde’s/sei whale in the Atlantic was in approximately 1,100 m water  
474 depth over the Blake Plateau east of central Florida, again much deeper than typical of the  
475 GOMx whales. Using 23 years of visual survey data from 1992-2014, Roberts et al. (2016) built  
476 habitat-based spatial density models for multiple cetacean species in U.S. waters of the western  
477 North Atlantic and GOMx. For the U.S. east coast, the authors utilized data collected from a  
478 variety of vessel- and aerial-based line transect surveys covering 895,000 km of effort from  
479 southern Florida to the Bay of Fundy. They predicted a mean monthly abundance of seven  
480 Bryde’s whales (C.V. = 0.58) along the entire eastern seaboard based on four Bryde’s/sei whale  
481 sightings recorded on these surveys (Roberts et al., 2016).

482  
483 Acoustic studies have also not recorded whale call types associated with any type of Bryde’s  
484 whale in the waters off Jacksonville, Florida, although fin, minke, *B. acutorostrata*, and sei  
485 whale vocalizations were detected (Frasier et al., 2016). Further north off Cherry Point, NC and  
486 in Norfolk Canyon, acoustic monitoring has detected several baleen whale species, but to date no  
487 Bryde’s whales have been recorded (Debich et al., 2014; Rafter et al., 2018). Overall, the  
488 evidence to date indicates Bryde’s whales are extremely rare in U.S. waters of the western North  
489 Atlantic.

490

491 Of great interest is whether the Bryde's-like whales from the GOMx are distributed outside of  
492 the GOMx in the Caribbean. In other areas of the western Atlantic, Bryde's whales have been  
493 recorded off Brazil (de Moura & Siciliano, 2012; Gonçalves et al., 2016; Lodi et al., 2015;  
494 Maciel et al., 2018), Suriname (de Boer, 2015) and north to at least Venezuela (Romero et al.,  
495 2001; Smultea et al., 2013), and into the southern Caribbean including waters of Bonaire (Debrot  
496 et al., 1998), Aruba (Luksenburg et al., 2015), and Curacao (Debrot, 1998; Debrot et al., 1998).  
497 Luksenburg et al. (2015) genetically identified the Aruba strandings as *B. e. brydei* and found  
498 they were genetically closest to the whales sampled off Madeira in the eastern Atlantic. Whales  
499 stranded in Brazil have also been genetically confirmed as *B. e. brydei* (Pastene et al., 2015).  
500 Finally, there is a record of a live stranded Bryde's whale (subspecies unknown) from St.  
501 Vincent and the Grenadines in 2009<sup>4</sup>.

502  
503 There are no comprehensive Caribbean-wide cetacean diversity studies from which to draw, and  
504 no Caribbean strandings north of Aruba have been genetically tested. However, based on  
505 existing sighting information it appears there is a hiatus of Bryde's whales in the central  
506 Caribbean, with *B. e. brydei* present in waters south of the hiatus and any Bryde's whale taxon  
507 generally rare north of it. A ship-board survey for cetaceans in 2000 covered waters from Puerto  
508 Rico to Venezuela (excluding Antigua and Barbuda, Dominica, and St. Vincent and the  
509 Grenadines) and recorded five Bryde's whale sightings, all in the southeastern Caribbean  
510 (Swartz & Burks, 2000), but which subspecies was seen is unknown. Similarly, Yoshida et al.  
511 (2010) surveyed from St. Kitts and Nevis south to Grenada and observed six Bryde's whales  
512 (subspecies unknown), all restricted to the southern survey area. One sighting was made in

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<sup>4</sup> Eastern Caribbean Cetacean Network. 2010. Marine Mammal Stranding Newsletter 2:7.

513 shallow waters northeast of Grenada while the remaining sightings were made in deep waters  
514 (2,000 m) of the Grenada and the Tobago basins. Additional surveys in the northern Caribbean  
515 have not recorded any subspecies of Bryde's whales (Roden & Mullin, 2000; Swartz et al.,  
516 2002).

517

518 Debrot et al. (2013) compiled cetacean records for the Dutch Windward Islands (Saba, St.  
519 Eustatius, St. Maarten, and the Saba Bank) and noted a surprising lack of records of any Bryde's  
520 whales. The authors suggested they may be absent from the northeastern Caribbean, a result in  
521 agreement with results from the shipboard surveys.

522

523 In the eastern Atlantic Ocean, Bryde's whales have been reported from the offshore islands of  
524 Cape Verde (Hazevoet & Wenzel, 2000), Madeira (Alves et al., 2010), and the Azores (Steiner et  
525 al., 2008). They also inhabit nearshore waters and offshore waters of the southwestern African  
526 coast (Best, 2001; Weir, 2010). To date, the whales in these regions have been genetically  
527 ascribed to Bryde's whales, *B. e. brydei*, (Luksenburg et al., 2015; Penry et al., 2018; Rosel &  
528 Wilcox, 2014), with the exception of whales in the Azores and the Gulf of Guinea, which have  
529 not yet been genetically tested. Thus, to date, these studies have supported the conclusion by  
530 Rice (1998) that Eden's whale (*B. e. edeni*) is not present in the Atlantic.

531

### 532 3.3.3 Stranding data

533 After compiling the available data from stranding reports from the GOMx and the U.S. Atlantic  
534 coast, we found 33 records that could potentially be Bryde's -like whales, 24 in the GOMx and 9  
535 in the Atlantic. We removed two of the GOMx records we identified as either duplicate records



536 or misidentifications (or both) (Table S3), leaving 22 stranding records in the GOMx listed as  
537 “Bryde’s whale,” dating as far back as 1954; of these, 11 were found in Louisiana at or east of  
538 the Mississippi River Delta, nine were collected along the GOMx coast of Florida, including the  
539 Everglades, and two were collected in western Louisiana (Fig. 4). Two stranded animals were  
540 recorded in the 1970s, seven in the 1980s, and four in 1990s, while three were recorded in the  
541 2000s and four in the 2010s. The remaining two were recorded in 1954 and 1965. We  
542 characterized the 22 strandings further (Table 4) as 1) “verified GOMx Bryde’s-like whale”  
543 when diagnostic DNA sequence data were retrieved from the specimen, 2) “Bryde’s-like whale”  
544 when stranding records included photos or written records indicating rostral ridges were present,  
545 but no genetic data were available, or 3) “unconfirmed Bryde’s-like whale” when, although the  
546 stranding was recorded as a Bryde’s whale, we could not find records (photos, written notes)  
547 indicating rostral ridges were present and no tissues were available. Whales in category 2 are  
548 most likely GOMx Bryde’s-like whales as we have found no genetic evidence for any other  
549 Bryde’s-like whale subspecies in the GOMx, and there is little reason to doubt the records from  
550 category 3 as being GOMx Bryde’s-like whales, but we chose to be conservative in our  
551 verification process. Following this categorization, we had tissue from seven and were able to  
552 confirm the mtDNA control region haplotype diagnostic of the Bryde’s-like whales from the  
553 GOMx in all seven, including the 1954 skull collected by Lowery (1954). Six Gulf strandings  
554 had photos that clearly showed rostral ridges indicative of all members of the Bryde’s whale  
555 complex, but no tissue was available for genetic analysis. The remaining nine could not be  
556 verified further than “baleen whale” following our conservative methods. Seven of those  
557 stranded in the northern GOMx in Louisiana, along the panhandle of Florida, or near Tampa,  
558 Florida where verified GOMx whale strandings are most common, suggesting it is likely these

559 were also GOMx Bryde's-like whales. Interpretations for the other two, one stranding in Big  
560 Pine Key, Florida and the other in western Louisiana, are more difficult.

561  
562 In the Atlantic, six of the nine records of "Bryde's whale" strandings included sufficient  
563 information to verify the animals were from the Bryde's whale complex, either because the  
564 records stated that photos were available to confirm rostral ridges or the skull or tissue was  
565 collected. Two of these six were confirmed genetically to match the Bryde's-like whales from  
566 the GOMx, having the diagnostic mtDNA control region haplotype. Three other records listed as  
567 Bryde's whale could not be confirmed either because decomposition of the carcass precluded  
568 observation of characteristic features of Bryde's whales or because the stranded animal was not  
569 documented well enough. Interestingly, all nine whales were relatively small; all but one was  
570 less than 1,000 cm in length (Table 4). Mead (1977) has suggested that the Bryde's whale  
571 strandings along the U.S. Atlantic were likely extralimital strays from the Gulf of Mexico.

572  
573 In addition to the records for the southern Caribbean mentioned previously, there are five  
574 stranding records for Bryde's whales in the northern Caribbean but the subspecies of each is  
575 unknown. These include a stranded Bryde's whale in Puerto Rico reported in Mignucci-  
576 Giannoni et al. (1999) and a record in the Division of Mammals Collections at the Smithsonian  
577 National Museum of Natural History of a stranding in the Bahamas on March 4, 2000 (STR  
578 12575) listed as "*B. edeni?*". There is a second record of a Bryde's whale stranding in the  
579 Bahamas in 2008 (Currie et al., 2019), and both the USNM database and the Southeast U.S.  
580 stranding database reference a May 1991 stranding of a Bryde's whale in St. Croix, Lesser  
581 Antilles (MME7994, SE6423). Additional information to verify these records was not found.

582 Whitt et al. (2011) reviewed records of marine mammals in Cuban waters and indicated one  
583 confirmed record of a Bryde's whale stranding from the southeastern coast of Cuba, but the  
584 subspecies is unknown. This animal was initially identified as a juvenile sei whale by Varona  
585 (1965). Mead (1977) re-classified it as a Bryde's whale as the bristles of the baleen were  
586 considered too coarse to be from a sei whale, although reports indicated no accessory ridges on  
587 the rostrum. Varona (1973), as reported in Whitt et al. (2011), suggested that sei whales were  
588 historically found off southeastern Cuba in the 1800s but it is possible these were  
589 misidentifications of Bryde's whales (Whitt et al., 2011).

590

591

#### 592 **4 | DISCUSSION**

593 Rosel and Wilcox (2014) revealed, based on a genetic analysis of mtDNA control region  
594 sequences compiled from a worldwide distribution, that the Bryde's-like whales found in the  
595 northern GOMx were evolutionarily distinct from all other lineages and indicated that they may  
596 deserve taxonomic status on par with the other members of the Bryde's whale complex, *B. e.*  
597 *edeni* and *B. e. brydei*. Augmenting this study with additional samples from the GOMx for  
598 genetic analysis and with the first morphological analysis an intact specimen from the GOMx  
599 further supports that these whales are taxonomically unique. The new morphological data  
600 provide a second, independent line of evidence as recommended for delimiting cetacean species  
601 (Reeves et al., 2004).

602

603 Several characteristics of the bones of the vertex of the skull distinguish the whales in the GOMx  
604 from all members of the Bryde's whale complex. They are clearly distinguished from Omura's

605 whales by the extent of the premaxilla, which do reach the frontal bones in the whales from the  
606 GOMx but not in Omura's whales. Bryde's-like whales from the GOMx are easily distinguished  
607 from Eden's whales, *B. e. edeni*, by fact that the frontals are only narrowly exposed between the  
608 ascending process of the maxilla and the supraoccipital. Finally, like *B. e. edeni* and *B. e. brydei*,  
609 the whales from the GOMx exhibit their own diagnostic shape of the nasal bones, and exhibit the  
610 unique feature of frontal bones wrapping around the smooth, curved posterior tips of the nasal  
611 bones and extending down in between the nasal bones, forcing a bigger gap between them than  
612 seen in the other subspecies. These features allow separation of Bryde's-like whales in the  
613 GOMx from Omura's whales and the two recognized subspecies of Bryde's whales.

614

615 Analysis of 18 new soft tissue samples and 1 bone sample, almost doubling the sample size used  
616 in the original analysis (Rosel & Wilcox, 2014), did not change the outcomes of the mtDNA  
617 genetic analysis or conclusion that these whales are genetically divergent from other whales in  
618 the genus *Balaenoptera*. Following the guidelines and standards for delimiting cetacean species  
619 and subspecies proposed by Taylor et al. (2017a), we find that the whales in the GOMx  
620 substantially exceed the recommended threshold for species for net nucleotide divergence (i.e.,  
621  $d_A > 0.02$ ). When compared to the two recognized subspecies of Bryde's-like whales and to the  
622 sei whale, values of  $d_A$  for Bryde's-like whales in the GOMx ranged from 0.10 to 0.13 (10 % -  
623 13 %) based on the first 375 bp of the mtDNA control region (Table 3). This level is equivalent  
624 to that seen between the two currently recognized subspecies of Bryde's whales ( $d_A = 0.10$ ).  
625 Thus, the whales from the GOMx are as divergent as the currently recognized subspecies are  
626 from each other (and all three exceed the threshold for species). Taylor et al. (2017a) also

627 recommended that, at the species level, two taxa must be diagnosably distinct, and specifically  
628 that there is a near 100% probability of identifying an individual as belonging to the taxon.  
629 Fixed nucleotide differences in the control region, such as exist between Bryde's-like whales  
630 from the GOMx and all other whales, serve to render them diagnosably distinct (100%), further  
631 meeting the quantitative criteria of being a separate species. Given the larger number of fixed  
632 differences in the control region (Table 3), additional mtDNA data, such as whole mitogenomes,  
633 is not likely to alter the diagnosability of these whales. In fact, Rosel and Wilcox (2014)  
634 identified multiple fixed differences in the cytochrome *b* and cytochrome oxidase I genes as  
635 well. For further perspective, Penry et al. (2018) compared mtDNA control region sequences  
636 from inshore and offshore ecotypes of Bryde's whale, *B. e. brydei*, off South Africa. Based on a  
637 1.8 – 2.1% divergence and ten fixed differences, they concluded the two ecotypes off South  
638 Africa represent different subspecies. The values for both metrics are an order of magnitude  
639 lower than those observed between the Bryde's whales-like in the GOMx and the two recognized  
640 subspecies, further illustrating the significant evolutionary divergence exhibited by the whales in  
641 the GOMx.

642

643 Phylogenetic analysis of the control region sequences continues to identify Bryde's-like whales  
644 from the GOMx as a unique lineage separated from the two Bryde's whale subspecies and from  
645 the sei whale and Omura's whale with strong support (Fig. 2). What the control region sequence  
646 data do not clearly answer is to which of the two subspecies these whales are most closely  
647 related. Posterior probabilities on the nodes joining the clades representing each taxon are very  
648 low, and in fact the phylogenetic tree based on the 375 bp alignment creates a trichotomy of the  
649 sei whale, *B. e. brydei*, and a joint *B. e. edeni* + GOMx whale clade, which itself has a posterior

650 probability of only 0.61, well below the threshold (0.90-0.95) recognized for robust conclusions  
651 concerning phylogenetic relationships (Huelsenbeck & Rannala, 2004). This result is not  
652 uncommon for the control region, which performs well at identifying unique taxonomic groups  
653 and, for instance is useful for DNA barcoding of cetacean species (Viricel & Rosel, 2012), but  
654 has been shown to have limitations in identifying evolutionary relationships among recently  
655 diverged cetacean taxa (e.g., Perrin et al., 2013). Further analyses utilizing a larger data set that  
656 includes nuclear DNA sequences will provide a more robust investigation of the evolutionary  
657 relationships among these taxa.

658

659 In addition to genetic and morphological data, Bryde's-like whales in the GOMx also have a  
660 unique acoustic signature that distinguishes them from all other baleen whales. Rice et al. (2014)  
661 recorded acoustic calls using marine autonomous recording units (MARUs) placed in the known  
662 whale habitat in the northeastern GOMx. Three types of sounds were recorded that were  
663 consistent with other baleen whale species, but none matched known sounds produced by other  
664 baleen whales, including the two Bryde's whale subspecies, suggesting these whales in the  
665 GOMx exhibit a unique and diagnostic acoustic repertoire; however, because the recorders were  
666 autonomous, it was not possible to directly link the recorded sounds to visual sightings of the  
667 whales (Rice et al., 2014). Širović et al. (2014) definitively identified a call-type directly  
668 associated with Bryde's-like whales in the GOMx through visual observation paired with towed  
669 acoustic-array recordings. More recently, long moans and downsweep pulse trains were  
670 validated to be from these whales in the GOMx using real-time visual and acoustic observations<sup>5</sup>.

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<sup>5</sup> M. Soldevilla, pers comm. National Marine Fisheries Service 75 Virginia Beach Drive, Miami FL, 33149. April 2019

671

672 A workshop on the taxonomy of cetaceans concluded that a single line of evidence (e.g., genetic  
673 data or morphological data) was sufficient to delimit cetacean subspecies while two independent  
674 lines of evidence were necessary for delimiting species (Reeves et al., 2004). Bryde's-like  
675 whales in the GOMx exhibit two strong lines of evidence that distinguish them from all other  
676 closely related species. Examination of morphological features of the skull key to discriminating  
677 among taxa in the Bryde's whale complex and Omura's whale (Wada et al., 2003), revealed  
678 multiple diagnostic characters that distinguish the whales in the GOMx from both *B. e. edeni* and  
679 *B. e. brydei*, and from Omura's whale. Similarly, the degree of genetic divergence between the  
680 whales in the GOMx and *B. e. edeni* and *B. e. brydei* ( $d_A > 0.10$ ) significantly exceeds the net  
681 divergence metric identified by Taylor et al. (2017a) for species delimitation based on mtDNA  
682 control region sequences ( $d_A > 0.02$ ), and multiple diagnostic sites in the mitochondrial sequence  
683 further support divergence at the species level. The apparent highly restricted range and  
684 isolation of these whales in the northern GOMx reinforces a severely limited opportunity for  
685 gene flow with any other populations of Bryde's whales, and the morphological differences rule  
686 out recent or ongoing male-mediated gene flow. The data presented here from multiple lines of  
687 evidence (genetics, morphology, distribution) indicate that the Bryde's-like whales in the GOMx  
688 are a previously unnamed species.

689

#### 690 **4.1 | Distribution**

691 The Bryde's-like whales in the GOMx are the only year-round resident baleen whale species in  
692 the GOMx. Sightings and strandings of all other baleen whale species in the GOMx are rare and

693 considered extralimital (Jefferson, 1995; Jefferson & Schiro, 1997). Compiling the sighting,  
694 acoustic, genetic, and stranding data, it is clear that these whales are restricted in their  
695 distribution to the GOMx, and that the northeastern GOMx, particularly the De Soto Canyon area  
696 and water depths of 150–410 m, are currently the primary habitat of these whales. The nearest  
697 confirmed populations of other members of the Bryde’s whale complex are of *B. e. brydei* in the  
698 southern Caribbean south to Venezuela and Brazil, and in the eastern North Atlantic and the  
699 eastern south Atlantic off South Africa (Alves et al., 2010; Best, 2001; de Boer, 2015; de Moura  
700 & Siciliano, 2012; Debrot, 1998; Debrot et al., 1998; Gonçalves et al., 2016; Hazevoet et al.,  
701 2010; Hazevoet & Wenzel, 2000; Luksenburg et al., 2015; Maciel et al., 2018; Pastene et al.,  
702 2015; Penry et al., 2018) (Fig. 5). To date there are no confirmed records of *B. e. edeni* from the  
703 Atlantic basin.

704  
705 LaBrecque et al. (2015) identified biologically important areas (BIAs) for cetacean species in the  
706 GOMx, including waters 100–300 m deep in an area in the northeastern GOMx for the GOMx  
707 whale [See Fig. 3.1 in LaBrecque et al. (2015)]. We have revisited and updated this area using  
708 additional years of sighting data to better reflect the currently known distribution in the  
709 northeastern GOMx (Figs. 4, 5). A convex hull polygon (IUCN, 2012) was drawn around all  
710 visual sightings recorded as “Bryde’s whale”, “Bryde’s/sei whale” or “balaenopterid whale” (the  
711 latter are cases where the characteristic rostral ridges of a Bryde’s whale were not noted),  
712 telemetry tag locations (n = 52) from a single Bryde’s-like whale tagged in 2010 (Soldevilla et  
713 al., 2017) in the northeastern GOMx, and Acousonde tag locations (n = 41) for one whale tagged  
714 in 2015 (Soldevilla et al., 2017); a total of 212 data points collected between 1989 and 2018.  
715 The convex hull polygon was trimmed at 410 m, determined based on the current deepest known



716 sighting of 408 m. By its very nature, many of the sightings fall on the boundary of the convex  
717 hull polygon and therefore the polygon under-estimates the range of the species and was further  
718 buffered to account for uncertainty in the distribution. A 10 km buffer was drawn around this  
719 polygon to capture the uncertainty in sighting position given the strip width of the vessel surveys.  
720 An additional 20 km buffer was then added to this "position uncertainty" to account for the likely  
721 movement of observed whales. This results in a 30 km buffer around sighting locations. The  
722 area should be updated periodically with new sighting data as they become available.

723

724 As mentioned above, there was a confirmed sighting of a Bryde's-like whale in the western  
725 GOMx in 2017 and there were two baleen whale sightings (only identified as "Bryde's/sei  
726 whale") during NMFS surveys in the western Gulf in the early 1990s. These sightings raise  
727 important questions. Is it possible that some whales move west from the current core habitat in  
728 the northeastern GOMx? Alternatively, do these sightings constitute remnants of a once more  
729 broadly distributed population, as suggested by whaling data (Reeves et al., 2011) and if so, why  
730 are they now rare in the western GOMx? Or do they come from another, as yet unidentified  
731 population in the southern GOMx? Has this area in the western GOMx become a marginal or  
732 suboptimal habitat for these whales? Further research in the western and southern GOMx will  
733 greatly aid our understanding of whether these whales utilize these habitats and if so, how often,  
734 and also how they are related to the whales that are found in the northeastern GOMx.

735

#### 736 **4.2 | Life History**

737 Little is known about the life history of these whales in the GOMx. Stranding and biopsy data  
738 indicate both sexes are present in the Gulf; the sex ratio determined for 32 individual whales

739 from the northern GOMx was 18 females and 14 males (not significantly different from a 50:50  
740 ratio, Chi-square with 1 degree of freedom,  $P = 0.4795$ ). In addition, stranding data indicate the  
741 whales are likely breeding in the GOMx, as we identified records of several smaller animals in  
742 the stranding records, including a 470 cm calf that stranded alive in November of 2006, and a  
743 693 cm individual that stranded in November of 1988 and was brought into captivity for a short  
744 time (Edds et al., 1993). In August 2016, two whales were sighted together in the northeastern  
745 GOMx core area during a NMFS SEFSC large-vessel survey. One whale was approximately  
746 half the size of the larger whale and had physical characteristics suggestive of a calf. In addition,  
747 a dead, lactating female whale was found in Tampa Bay in October of 2009. This whale  
748 mortality likely resulted from a ship strike as the whale exhibited internal injuries consistent with  
749 blunt force trauma.

750

751 Basic information on total length, standard external measurements, external color pattern, etc.  
752 suffers from inadequate sample sizes. After re-examining records for strandings recorded as  
753 “Bryde’s whales” in the GOMx and western North Atlantic, and removing those we determined  
754 to be mis-identified or duplicate records, some external measurements were available in common  
755 across eight whales (Table S4). Total length measurements for these whales ranged from 470 cm  
756 to 1,265 cm.

757

758 Worldwide, members of the Bryde’s complex exhibit a variety of foraging strategies and prey  
759 preferences, often with observations of surface feeding. Overall, pelagic schooling fishes in the  
760 order Clupeiformes (sardines, herring, menhaden, anchovies) are the most commonly recorded  
761 prey, along with similar schooling species such as members of the family Carangidae (Best,

2001; Konishi et al., 2009; Murase et al., 2007; Siciliano et al., 2004; Tershy, 1992; Watanabe et al., 2012). Populations examined further offshore also target euphausiids (Best, 2001; Konishi et al., 2009), while the *B. e. brydei* population of the Hauraki Gulf in New Zealand appears to prey on copepods and krill along with ray-finned fishes and salps (Carroll et al., 2019). However, diet is poorly characterized for the whales in the GOMx. Surface feeding has never been observed. Recently, Soldevilla et al. (2017) placed an Acousonde suction-cup tag on a Bryde's-like whale in the northeastern GOMx. The tag remained attached for nearly three days (63.85 h) in October 2010 and revealed a diel diving pattern. During the night, the whale remained near the surface, 88% of the time within 15 m of the surface. Daytime dive behavior was characterized by repeated deep dives to depths >200 m, likely at or near the seafloor. Some of these deep dives included lunges near the seafloor associated with foraging (Soldevilla et al., 2017). This type of bottom feeding is unusual for members of the complex. It is not known what they may have been feeding on at those depths. Lanternfish (Myctophidae) and hatchetfish (Sternoptychidae) are abundant members of pelagic waters of the GOMx (Ross et al., 2010; Stickney & Torres, 1989), and some species may serve as prey. Further work to identify primary prey species and foraging behaviors is needed and will be important for identifying potential threats and important habitat for these whales.

Finally, estimates of abundance for the whales in the northern GOMx are under 100 individuals. Broad-scale aerial and ship-based line transect surveys to estimate cetacean abundance have been conducted in the northern GOMx as far back as 1991. Eleven abundance estimates have been made between 1991 and 2009 and range between zero and 44 [See Rosel et al. (2016) for summary of surveys]. Surveys with the lowest estimates covered waters primarily of the western

785 GOMx, supporting their rarity in this region. It should be noted, however, none of these surveys  
786 were focused on estimating abundance of a rare species and precision of all estimates is poor.  
787 The current best estimate of abundance is 33 (CV = 1.07) (Waring et al., 2015). Future work  
788 dedicated to estimating abundance within the known habitat in the northeastern GOMx is  
789 needed.

790

### 791 **4.3 | Conservation status**

792 The small population size and associated deleterious genetic effects (e.g., inbreeding depression,  
793 loss of potentially adaptive genetic diversity and accumulation of deleterious mutations), and the  
794 restricted distribution alone, place these whales at high risk of extinction and they are of grave  
795 conservation concern. They recently have been listed as Endangered under the U.S. Endangered  
796 Species Act of 1973 and are listed as a Critically Endangered subpopulation on the IUCN Red  
797 List (Corkeron et al., 2017). Additional significant threats include vessel collisions,  
798 anthropogenic noise during seismic surveys, habitat destruction, modification or curtailment of  
799 habitat range during energy exploration and development, oil spills and oil spill response, and  
800 marine debris (Rosel et al., 2016). Fishery interactions may also pose a threat, but more research  
801 is necessary to determine the level of impact from this threat (Rosel et al., 2016; Soldevilla et al.,  
802 2017). The recent analyses of dive behaviors by Soldevilla et al. (2017) indicate these whales  
803 may feed near the seafloor in a region where some bottom longline fishing occurs, raising the  
804 risk of fishery interactions. The surface behavior identified by the same study suggests these  
805 whales may spend a considerable amount of time at night within the first 15 m of the water  
806 column. This behavior significantly raises the risk of ship strikes. Two whales have shown  
807 evidence for ship strike. An adult, lactating female stranded in Tampa Bay, Florida with injuries,

808 including separated vertebral, lung damage, and subdermal contusions, consistent with impact  
809 caused by a large object. In 2019, a free-swimming whale was observed in the northeastern  
810 GOMx with a severely deformed spine posterior to the dorsal fin consistent with a vessel strike  
811 (Fig. 6). These two cases illustrate the anthropogenic threat that vessels may pose to this  
812 population. Finally, the 2019 whale that stranded in the Everglades (FMMSN1908, USNM  
813 594665) was found to have a sharp piece of intragastric plastic approximately 6.6l x 6.2w x 0.2d  
814 cm in dimension. The plastic caused hemorrhaging and acute gastric necrosis in the second  
815 stomach chamber. The whale was thin and because the necropsy identified no other infections or  
816 pathologies that could be attributed to the animal's death, it was concluded that the ingestion of  
817 the plastic led to the stranding and subsequent mortality of this whale.

818  
819 Continued efforts to fully characterize dive behavior, feeding strategies, and prey preference will  
820 improve management strategies for this Endangered whale. In addition, ongoing research to  
821 determine whether they regularly use habitat in the western and/or southern GOMx will aid our  
822 understanding of their distribution. If they are shown to use these waters with regularity, further  
823 work to determine the relationship of such whales to those utilizing the northeastern GOMx is  
824 critical to developing a full picture of the status and range of these whales. Finally, a better  
825 understanding of whether they once were a component of the ecosystem in the north-central and  
826 western GOMx, as suggested by Reeves et al. (2011) based on Yankee whaling records, prior to  
827 the extensive alteration of habitat through energy exploration and development is needed. If they  
828 previously utilized habitat in the western GOMx, understanding why they may have abandoned  
829 the habitat will significantly aid conservation and recovery plans for these whales.

830

831 **4.4 | Conclusion**

832 The data presented here provide multiple lines of evidence (genetics, morphology, distribution)  
833 indicating that the Bryde’s-like whales in the GOMx are a previously unnamed species. The  
834 morphological and genetic lines of evidence that distinguish these whales in the GOMx as a new  
835 species also provide equivalent support for re-elevating the two subspecies of *B. edeni* to species  
836 level, *B. edeni* Anderson, 1879 and *B. brydei* Olsen, 1913. Here, the only species that would  
837 then utilize the English name Bryde’s whale would be *B. brydei*, the larger, more pelagic  
838 balaenopterid distributed world-wide in tropical and subtropical oceans. Eden’s whale would  
839 refer to *B. edeni*, the smaller animals found, to date, in coastal and shelf waters of the tropical  
840 and subtropical Indian and western Pacific Oceans. The terms “Bryde’s-like whale” and  
841 “Bryde’s whale complex” would not be necessary any more. Future investigation of other  
842 coastal populations, such as the population off the coast of south Africa (Best, 1977; Best, 2001;  
843 Penry et al., 2018) may continue to identify new subspecies.

844

845 We recognize the lingering unfinished, but ongoing, taxonomic work in this group, i.e.,  
846 genetically verifying the holotype of *B. edeni* and the need to identify and designate a neotype  
847 specimen and its associated genetic signature for *B. brydei*. Some may not yet support species  
848 rank for these lineages, but might rather support continued recognition of subspecies status until  
849 these underlying taxonomic details are worked out. However, a convincing volume of evidence,  
850 both morphological and genetic, has grown substantially in recent years (Kershaw et al., 2013;  
851 Penry et al., 2018; Rosel & Wilcox, 2014; Sasaki et al., 2006; Wada et al., 2003; Yamada et al.,  
852 2006; Yamada et al., 2008) and multiple independent lines of evidence are consistent with

853 species level differences for all members of the “Bryde’s whale complex” and now for the new  
854 evolutionarily distinct species found in the GOMx.

855

#### 856 **4.5 | Systematics**

857

858 Order Cetartiodactyla Montgelard, Catzefils and Douzery, 1997

859 Cetacea Brisson, 1762

860 Family Balaenopteridae Gray, 1864

861 Genus *Balaenoptera* Lacépède, 1804

862 *Balaenoptera ricei* sp. nov.

863 Rice’s whale

864 Figs. 3, 7, 8; Table 1; Figs. S8 – S10

865

866

867 *Holotype and Type Locality*

868 594665, an adult male, 1,126 cm, stranded on 29 January 2019 near

869

870 The skull (Figs. 7, S10) and complete skeleton and baleen are deposited in the

871 The full mtDNA control region sequence for the holotype

872 has been placed in GenBank with accession number MN017985.

873

874 *Additional Material*

875 Lowery (1974) reported a skull found on the Chandeleur Islands, St. Bernard Parish, Louisiana  
876 in June 1954. This specimen is housed in the Louisiana State University Museum of Natural  
877 Science (LSUMZ 17027) and was originally identified as a fin whale. We sequenced the  
878 mitochondrial DNA control region of this specimen and identified it as a Rice's whale.  
879 Unfortunately, the skull is missing a number of important bones, including the premaxillae,  
880 nasals, lacrimals, jugals, and pterygoid hamuli. Photographs of the skull are in Lowery (1974)  
881 and Figs. S3, S4.

882

883 A complete skull and skeleton of a 1,105 cm immature male whale that stranded in New  
884 Hanover County, North Carolina (34.07° -77.88°) on March 13, 2003 was deposited in the  
885 The whale was  
886 genetically confirmed to be a Rice's whale (Rosel & Wilcox, 2014). Best (2007) published  
887 photographs of the skull of this specimen and assigned it as *B. edeni*. Photographs of the skull  
888 are also in Fig. S5.

889

890 On 4 October 2009, a 1,265 cm adult female whale stranded in Tampa Bay, Florida (27.91° -  
891 82.43°) and the carcass was buried in Fort De Soto Park, Pinellas County, Florida. The whale  
892 was genetically confirmed as a Rice's whale (Rosel & Wilcox, 2014). In March 2018, the  
893 remains were excavated in the hopes of finding an intact skull to serve as a type specimen.  
894 Unfortunately, the skull had been crushed during burial and most of the specimen lay in water  
895 for the nine years it was buried. The remains of the skull and a nearly complete vertebral column  
896 were retrieved and deposited in the Florida Museum of Natural History in Gainesville, Florida  
897 with accession number UF33536.



898

899 *Diagnosis*

900 *Balaenoptera ricei* differs from *B. e. edeni* and *B. e. brydei* in the following morphological  
901 features: the nasals taper and curve laterally at the posterior end and have a smooth margin,  
902 meeting the medial-posterior margin of the ascending process of the maxilla; there is a broad gap  
903 between the nasal bones that does not narrow posteriorly created in part by the frontal bones  
904 which protrude anteriorly between the posterior end of the nasals (Fig. 8). Rice's whale can also  
905 be differentiated from all other species of rorqual baleen whales based on molecular genetic  
906 characters, as shown in the phylogenetic analyses of the mtDNA control region (Table 3, Fig. 2).  
907 Within the 305 base pair alignment of the 5' end of the mtDNA control region, ten diagnostic  
908 sites differentiate *B. ricei* from both *B. e. brydei* and *B. e. edeni* (Table 2).

909

910 *Description*

911 The Rice's whale is a medium-sized rorqual whale. They appear to be larger than Omura's  
912 whales and smaller than Bryde's whales, *B. e. brydei*, but, based on limited samples, about the  
913 same size as Eden's whales. To date, the largest verified Rice's whale was 1,265 cm in length (a  
914 lactating female) and the largest male was 1,126 cm. Rice's whales have a falcate dorsal fin  
915 (Fig. S6). In the holotype specimen, the dorsal fin was located approximately 2/3 of the way  
916 back from the snout. The flippers are uniformly dark. Although sample sizes are small, the  
917 ventral grooves/pleats reach to or just past the umbilicus; in the holotype specimen 1 pleat  
918 extended 36 cm past the umbilicus and two additional pleats extended past the umbilicus but  
919 were not measured (Table S4). The number of pleats counted on the holotype specimen at the

920 flipper insertion was 27 to the central midline making a total of 54 pleats. These whales exhibit  
921 no external asymmetrical pigmentation on the lower jaws, thereby differentiating them from the  
922 asymmetrical jaw coloration seen in fin whales and Omura's whales. Body color is uniformly  
923 dark charcoal gray above, including both the upper and lower jaws, and light to pinkish  
924 countershading ventrally. Some whales exhibit diffuse white washes on the body around the  
925 base of the dorsal fin and/or along the sides but to date no consistency in the pattern across  
926 individuals has been seen (Fig. S7). The fringe of the baleen plates is uniformly cream colored  
927 throughout the entire rack, the anterior baleen plates are cream colored on both sides, with a  
928 distinct posterior transition to black plates (Fig. 3). Plate count for the holotype specimen was  
929 264 on the left side. A total of 224 plates were counted on the right side but approximately 60  
930 cm of the baleen rack of the right side was not accessible making this is an incomplete count.  
931 Mead (1977) and Kato and Perrin (2018) indicated that the baleen bristles of members of the  
932 Bryde's whale complex are coarser than those of sei whales, and we can confirm, based on a  
933 sample size of three, that the baleen bristles of Rice's whales from the GOMx are coarser than  
934 that of a sei whale that stranded in the GOMx in 1994. However, no comprehensive analysis of  
935 bristle diameter across all the Bryde's whale taxa has yet been performed.

936

937 The vertebral formula of the holotype is cervical (7) + thoracic (13) + lumbar (13) + caudal (20)  
938 = 53. There were 13 ribs on either side and the head of each first rib is bifurcated.

939

940 Several other unique features were noted in the skeleton of the holotype. Junge (1950),  
941 Lönnberg (1931), and Omura (1959) describe the stylohyal bones of Bryde's whales as generally  
942 longer than they are wide with some degree of curvature. The stylohyal bones of the holotype of

943 *B. ricei* had little curvature to them and are very broad (Fig. S9). In addition, the pelvic bones of  
944 the holotype specimen are nearly straight, with only a very small projection on one side (Fig.  
945 S9).

946

#### 947 *Etymology*

948 The specific name, *ricei*, is in honor of renowned American cetologist Dale W. Rice (1930-  
949 2017). We choose this species name to commemorate Dale W. Rice who had a distinguished 60-  
950 year career in marine mammal science and wrote the seminal volume “Marine Mammals of the  
951 World” (Rice, 1998), which provided the first comprehensive worldwide review of the  
952 systematics and distribution of all marine mammal species. He was the first researcher to  
953 recognize that Bryde’s whales are present in the GOMx (Rice, 1965). We propose Rice’s whale  
954 as the common English name. Naming it after a person is consistent with the other members of  
955 the complex: Eden’s whale (*B. e. edeni*) having been named after Ashley Eden, a British  
956 Commissioner (Anderson, 1878 [1879]), Bryde’s whale (*B. e. brydei*) named after Johan Bryde,  
957 a Norwegian businessman and whaler (Olsen, 1913), and Omura’s whale (*B. omurai*) was named  
958 after the Japanese cetologist Hideo Omura (Wada et al., 2003). We note that the common name  
959 ‘Gulf of Mexico whale’ has been used for this species.

960

#### 961 *Nomenclatural Statement*

962 A Life Science Identifier (LSID) was obtained for this publication:

963

964

965 *Comparison*

966 Externally, Rice's whale is separated from all other balaenopterid whales except those in the  
967 Bryde's whale complex by the presence of three longitudinal ridges on the rostrum; one in the  
968 center and two lateral ridges (Fig. 1). Omura's whale lacks these prominent lateral ridges,  
969 instead having faint ridges visible only in certain viewing conditions (Cerchio et al., 2015).

970

971 As described in Wada et al. (2003), the vertex of the skull, including the shapes and extent of the  
972 ascending process of the maxilla (APM), the nasals, frontals, premaxillae serve as much of the  
973 defining morphological characteristics that separate members of the Bryde's whale complex  
974 (Fig. 8). In this region, *B. ricei* is clearly differentiated from *B. e. edeni* by the shape and extent  
975 of the ascending process of the maxilla which broaden only slightly at the posterior end, more  
976 similar in shape to *B. e. brydei* than *B. omurai* or *B. e. edeni*, with *B. e. edeni* being distinctive in  
977 its slender ascending process of the maxilla with rounded posterior end (Fig. 8, S10). *B. ricei*  
978 also differs from *B. e. edeni* in the shape of the nasals (triangular versus rectangular), and the  
979 extent of the frontals, which are exposed as a thin strip or belt between the ascending processes  
980 of the maxilla, the posterior end of the nasals and the supraoccipital, rather than the broad  
981 exposure of the frontals seen in *B. e. edeni*. *B. ricei* is most easily differentiated from *B. omurai*  
982 by the posterior end of the premaxillae which reach the frontals in *B. ricei* but not in *B. omurai*  
983 (Fig. 8). In addition, the alisphenoid is in contact with the squamosal (Fig. S8) while it is  
984 separated from the squamosal bone in *B. omurai* (Wada et al., 2003). Finally, *B. ricei* can be  
985 distinguished from *B. e. brydei* by the shape of the posterior end of the nasals which curve  
986 laterally and have smooth margins, while in *B. e. brydei* the posterior end of the nasals remains  
987 relatively straight and the posterior margin is crenulated. In addition, the frontal bones wrap

988 around and extend anteriorly into the space between the posterior end of the nasals, creating a  
989 significant space or gap between the nasal bones along their entire length.

990

991 Finally, *B. ricei* is unambiguously discriminated from all other balaenopterid whales by DNA  
992 sequence of the mitochondrial genome. Ten diagnostic sites in the 5' end of the mitochondrial  
993 control region (between nucleotide positions 15536-15818 of the *B. e. brydei* mtDNA genome  
994 GenBank accession number AB201259) separate *B. ricei* from all members of the Bryde's whale  
995 complex (Table 2). Similarly, mitochondrial cytochrome *b* and cytochrome oxidase I genes  
996 exhibit multiple fixed differences between *B. ricei* and *B. e. edeni*, *B. e. brydei*, and *B. omurai*  
997 (Rosel & Wilcox, 2014).

998

#### 999 *Distribution*

1000 Based on vessel and aerial survey sightings, the primary core habitat of Rice's whale is currently  
1001 in the northeastern GOMx, centered over the De Soto Canyon in waters between 150 and 410 m  
1002 depth (Fig. 4). Recently there was a genetically confirmed sighting in the western GOMx off the  
1003 central Texas coast in 225 m water depth (National Marine Fisheries Service, 2018), and  
1004 preliminary analysis of acoustic recordings from the western GOMx along the shelf break south  
1005 of the Flower Garden Banks National Marine Sanctuary suggest the presence of Bryde's-like  
1006 whales<sup>6</sup> in the same area as two balaenopterid sightings made by NMFS in the early 1990s (Fig.  
1007 4). While contemporary sightings are primarily confined to the northeastern GOMx, it is  
1008 possible the species historically had a broader distribution in the GOMx. Reeves et al. (2011)

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<sup>6</sup> M Soldevilla, pers comm. National Marine Fisheries Service 75 Virginia Beach Drive, Miami FL, 33149. April 2019

1009 reviewed whaling logbooks from the GOMx and identified records of “finback” whales from the  
1010 north central Gulf south of the Mississippi River delta and in the southern Gulf on the Campeche  
1011 Banks. As fin whales are not part of the GOMx ecosystem, these were likely Rice’s whales  
1012 misidentified as fin whales (Reeves et al., 2011), suggesting the whale’s distribution was broader  
1013 than we see today.

1014

1015

1016 **ACKNOWLEDGMENTS**

1017 The work presented here is the culmination of decades of work by many dedicated and  
1018 committed people. First, we acknowledge and sincerely thank Blair Mase, NMFS Southeast  
1019 Fisheries Science Center, and Denise Boyd, Florida Fish and Wildlife Conservation  
1020 Commission, who, along with a dedicated crew of volunteers including staff from Everglades  
1021 National Park, responded to and secured the January 2019 Rice's whale that stranded in  
1022 Everglades National Park and serves as the type specimen for this whale. In addition, Fort De  
1023 Soto Park in Florida kindly provided a location to bury the whale and hold the specimen for  
1024 cleaning. We thank John Ososky, Michael McGowen, and the U.S. Natural Museum of Natural  
1025 History at the Smithsonian Institution who helped move the specimen for further preparation,  
1026 conducted final preparation, and allowed us to deposit the specimen into the Museum's  
1027 collection.

1028 Searches through old archives, databases and paper files for stranding records, observational  
1029 data, and sightings data could not have been possible without help from the following people to  
1030 whom we thank with great gratitude: Gina Rappucci and Elizabeth Stratton, NMFS Southeast  
1031 Fisheries Science Center; James Mead, Charles Potter, Division of Mammals, Smithsonian  
1032 Institution National Museum of Natural History; Nicole Vollmer, NOAA/NMFS/National  
1033 Systematics Laboratory and Smithsonian Institution National Museum of Natural History. Lance  
1034 Garrison and Melissa Soldevilla, NMFS Southeast Fisheries Science Center, were critical in  
1035 organizing and implementing many of the SEFSC surveys and acoustic studies, respectively, that  
1036 resulted in new information on this whale. As chief scientist for multiple cruises, Anthony  
1037 Martinez, NMFS Southeast Fisheries Science Center, was instrumental in collecting much of the  
1038 at sea information, biopsies, photos, and video for these whales in the northern Gulf of Mexico

1039 and, with Elizabeth Josephson and Lisa Conger, Northeast Fisheries Science Center, collected  
1040 the overhead photo; Laura Dias, NMFS Southeast Fisheries Science Center, searched our  
1041 archives for photos from NMFS vessel surveys. We also thank Luis Pastene, Institute of  
1042 Cetacean Research, and Gwenith Penry, Nelson Mandela University, for providing valuable,  
1043 unpublished control region sequence data and haplotype information. William McLellan,  
1044 University of North Carolina at Wilmington, provided external measurements from the stranded  
1045 whale in North Carolina, and Nicole Vollmer and Christine Favorito, George Washington  
1046 University, provided images of the whale's skull, USNM 572922. Deborah Epperson provided  
1047 the Protected Species Observer data from BOEM.

1048         We thank Jacob A. Esselstyn and Donna Ditman, Louisiana State University, for access  
1049 to the LSU Museum of Natural History's collection to examine, photograph and ultimately  
1050 sample for DNA analysis the 1954 Rice's whale specimen. Cheryl Munday and the NMFS  
1051 Southeast Regional Office organized the effort, led by Keith Rittmaster, North Carolina  
1052 Maritime Museum and Robert Bonde, United States Geological Survey, to exhume the whale  
1053 that stranded in 2009 and was buried in Fort De Soto Park in Florida. Verity Mathis and the  
1054 Florida Museum of Natural History kindly accepted into their collection the bones that were  
1055 recovered. Yuko Tajima, National Museum of Nature and Science, Japan, and Kent Mori, The  
1056 Museum on the Street Association, provided invaluable comments and insight on the  
1057 morphological features of the holotype and Kent Mori provided access to a 3-dimensional  
1058 rendering of the holotype skull. All photography and biopsy sampling by NMFS were conducted  
1059 under MMPA permits issued to the NMFS Southeast Fisheries Science Center. We thank R.  
1060 Brownell, E. Archer, E. Fordyce, and two anonymous reviewers for comments and suggestions  
1061 that helped improve the manuscript. The scientific results and conclusions, as well as any views



1062 or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of  
1063 NOAA or the Department of Commerce.

1064

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1418  
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1420 Figure Legends

1421

1422 Figure 1. Aerial photograph of a Bryde's-like whale in the northeastern Gulf of Mexico. Photo  
1423 credit: NMFS SEFSC and NEFSC under MMPA permit.

1424

1425 Figure 2. Bayesian reconstruction of phylogenetic relationships among members of the Bryde's  
1426 whale complex based on 375 bp control region alignment. Posterior probabilities > 0.90 are  
1427 shown at nodes. Haplotypes with a \* indicate individuals morphologically identified to species  
1428 by Sasaki et al. (2006) and used to identify the species clades. Length of scale bar is  
1429 proportional to the number of nucleotide substitutions per site. GenBank accession numbers as  
1430 well as geographic localities where the haplotype has been recorded are included in haplotype  
1431 labels (Atlantic Ocean: WNA = western North Atlantic, ENA = eastern North Atlantic, ESA =  
1432 eastern South Atlantic, GOMex = Gulf of Mexico, CAR = Caribbean Sea; Pacific Ocean: WNP  
1433 = western North Pacific, ENP = eastern North Pacific, WSP = western South Pacific, ESP =  
1434 eastern South Pacific, CSP = central South Pacific, ECS = East China Sea, SCS = South China  
1435 Sea, SOJ = Sea of Japan; Indian Ocean: NIO = northern Indian Ocean, WIO = western Indian  
1436 Ocean, EIO = eastern Indian Ocean; Southern Ocean: SO). See Table S1 for all sequences that  
1437 were collapsed to each haplotype.

1438

1439 Figure 3. Images from the whale that stranded January 2019 in the Gulf of Mexico (holotype  
1440 specimen USNM 594665, FMMSN1908). (a) ventral view of body; (b, c) right rack of baleen  
1441 and close up of anterior portion of the rack; (d) right flipper; (e) ventral and (f) dorsal view of the

1442 fluke. Scale bar is 10 cm. Photos in 3b and 3c were inverted so the dorsal side is up. Photo  
1443 credit: Florida Fish and Wildlife Conservation Commission.

1444

1445 Figure 4. Distribution of all sightings and strandings of Bryde's-like whales in the Gulf of  
1446 Mexico and Atlantic U.S. EEZ. All visual survey sightings (blue circles) recorded as "Bryde's",  
1447 "Bryde's/sei" and '*Balaenoptera* sp.'" whales during NMFS vessel and aerial surveys from 1992  
1448 to 2019, including all sightings listed as "Bryde's/sei whales" or "*Balaenoptera* sp." in the  
1449 western North Atlantic and sightings recorded by protected species observers (PSO) on seismic  
1450 vessels (yellow circles) that could potentially have been a baleen whale. All strandings recorded  
1451 as "Bryde's whales" (red triangle; presence of rostral ridges confirmed in stranding record or  
1452 photos) or unconfirmed Bryde's-like whale (black circle; could not confirm presence of rostral  
1453 ridges in stranding record), and genetically confirmed Gulf of Mexico Bryde's-like whale (green  
1454 square) through May 2019, including the extralimital strandings in the western North Atlantic.  
1455 Green polygon represents the core habitat for the Bryde's-like whales in the northeastern Gulf of  
1456 Mexico. The 100 m, 200 m, 400 m and 1000 m isobaths and the U. S. EEZ are shown.

1457

1458 Figure 5. Localities of published Bryde's-like whale observations in the greater Atlantic Ocean.  
1459 Brown circles represent observations that were also genetically identified as *B. edeni brydei*.  
1460 Blue circles represent observations that did not include genetic information. Green polygon  
1461 represents core habitat identified in the northeastern Gulf of Mexico.

1462

1463 Figure 6. Deformation to tail stock, possibly resulting from a ship strike in a Bryde's-like whale  
1464 from the northern Gulf of Mexico. Photo credit: NMFS SEFSC under MMPA permit.

1465

1466 Figure 7. Images of (a) dorsal, (b) ventral, (c) right lateral, and (d) caudal views of the skull of

1467 Rice's whale (holotype specimen USNM 594665).

1468

1469 Figure 8. Vertex of the skulls of (a) Eden's whale, *B. e. edeni* (RMNH4003), (b) Rice's whale, *B.*

1470 *ricei* (USNM 594665, holotype), (c) Bryde's whale, *B. e. brydei* (CKU HL19990729), and (d)

1471 Omura's whale, *B. omurai* (NSMT M32505). pmx = premaxilla, na = nasal, asp = ascending

1472 process of the maxilla, fr = frontal, oc= occipital.

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1477 Table 1. Ten measurements of the skull of USNM 594665 (holotype).

Measurement	Length (cm)	Comments
Condylbasal length	284.4	right side as left premaxilla is broken
Maxillary length	204.5	right side as left premaxilla is broken
Zygomatic width	142.6	
Exoccipital width	101.6	
Occipital condyle width	25.1	
Rostrum width at antorbital notch	86.7	
Maximum nasal width	18.8	
Maximum nasal length	32.9	right side
Occipital shield length	63.6	straight/parallel measurement

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1483 Table 2. Characteristic attributes (CAs) analysis of the control region (305 bp) for Bryde’s-like  
 1484 whales and Omura’s whale identifying 30 diagnostic sites. n: total number of individuals used in  
 1485 the analysis for each taxon. Grayed cells identify sites diagnostic for a species. Nucleotide  
 1486 positions 15536-15818 correspond to the *B. e. brydei* mtDNA genome of GenBank accession  
 1487 number AB201259.

	15536	15554	15556	15563	15564	15565	15569	15573	15574	15575	15578	15585	15588	15592	15605	15608	15609	15613	15616	15621	15623	15624	15660	15671	15672	15735	15756	15769	15816	15818	
<i>B. e. brydei</i> (n = 629)	C	A	T	T	T	T	C	T	A	T	A	C	A	T	T	C	T	G	G	A	A	T	T	G	C	A	C	A	C	C	
<i>B. e. edeni</i> (n = 67)	*	*	*	C	*	*	*	*	*	*	*	*	*	C	*	*	C	*	T	*	*	*	*	*	*	*	*	*	T	*	*
GOMx whales (n = 36)	*	*	*	*	C	*	*	*	*	*	*	T	*	*	*	T	C	*	T	*	G	C	*	*	*	G	T	C	T	G	
<i>B. omurai</i> (n = 41)	T	G	C	*	*	C	T	C	T	C	G	*	G	*	C	*	C	A	T	G	*	*	C	T	A	*	*	T	*	*	

1488  
 1489

1490 Table 3. Genetic divergence estimates for Bryde's-like, sei and Omura's whales based on the 375  
 1491 bp alignment of the mitochondrial DNA control region. Number of individuals (n), number of  
 1492 haplotypes (h). Net between group divergence ( $d_A$ , Nei 1987) corrected using the T3P model is  
 1493 below diagonal, within group divergence is along diagonal, and number of fixed differences  
 1494 (number of indels) between taxa above the diagonal.

	n	h	GOMx whales	<i>B. e.</i> <i>edeni</i>	<i>B. e.</i> <i>brydei</i>	<i>B.</i> <i>borealis</i>	<i>B.</i> <i>omurai</i>
GOMx whales	36	2	0	25	24	22 (1)	51 (8)
<i>B. e. edeni</i>	22	5	0.103	0.009	20	20 (1)	42 (8)
<i>B. e. brydei</i>	27	15	0.128	0.102	0.019	17 (1)	39 (5)
<i>B. borealis</i>	90	10	0.114	0.102	0.083	0.016	41 (9)
<i>B. omurai</i>	17	5	0.304	0.229	0.246	0.264	0.004

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Table 4. Compilation of unconfirmed Bryde’s-like whale (identified in stranding record as a baleen whale or “Bryde’s whale” but no description or photos to confirm presence of rostral ridges), Bryde’s-like whale (identified in stranding record as a “Bryde’s whale” and with written description or photos to confirm presence of rostral ridges), and verified Gulf of Mexico Bryde’s-like whale (confirmed via genetic analysis) strandings in the northern Gulf of Mexico and U.S. eastern seaboard. Lengths are noted as being actual measured length (a) or estimated lengths (e) as noted in the stranding data records.

Catalog Number	Additional Identifiers	Date (mm/dd/yy)	Location	Lat (dd)	Long (dd)	Length (cm)	Sex	Verification	Data and Source for Verification	Additional Citations
<b>Gulf of Mexico</b>										
LSUMZ 17027	STR338	June 1954	Chandeleur Islands, St. Bernard Parish, LA	29.83	-88.83	n/a	n/a	verified GOMx Bryde’s-like whale	genetics; present study	Lowery 1974; Mead 1977; Schmidly 1981; Jefferson 1995
MME 2		8/18/82	2 km SE of Isle au Pitre, LA	30.13	-89.18	1,500 (e)	n/a	unconfirmed Bryde’s-like whale	no photos or notation of rostral ridges	Jefferson 1995
SEAN 7128		12/25/82	Southwest Pass, LA	29.03	-89.32	1,160 (e)	n/a	unconfirmed Bryde’s-like whale	no photos or notation of rostral ridges	Jefferson 1995
MME 1486	SE2250	11/8/85	Chandeleur Islands, Near Palos Island, LA	29.79	-88.89	1,040 (a)	M	unconfirmed Bryde’s-like whale	Top of head could not be accessed, cannot confirm ridges present. Ventral grooves reach to umbilicus. Likely Bryde's whale	Jefferson 1995
MME 1939	SE2589, MME01956	10/28/86	Cameron Parish, LA	29.77	-93.33	990 (e)	M	Bryde's-like whale	photos show ridges; Harris 1987	Harris and Richard 1987; Jefferson 1995
MME 5967	SE4790; 90-1-1	1/8/90	Freshwater Bayou Canal, 1/2 Mile West of Mouth, Intracoastal City, LA	29.53	-92.32	1,067 (e)	n/a	unconfirmed Bryde’s-like whale	no photos or notation of rostral ridges	Jefferson 1995
MME 6574	SE5716, MM9101	1/7/91	1/4 M West of Bunces Pass, Saint Petersburg, FL	27.65	-82.75	1,120	n/a	unconfirmed Bryde’s-like whale	no photos or notation of rostral ridges	Jefferson 1995

MME 7822	SE6168, MME7822, DRC-91-09	5/24/91	No Name Key, in Bogie Channel/ Big Pine Key, or Grassy Key, FL	24.72	-81.35	1,140/ 1,158 (e)	n/a	unconfirmed Bryde's-like whale	no photos or notation of rostral ridges	Jefferson 1995
MME 8837	SE8092, LA001-93	6/14/93	Le Petit Pass Island, LA	30.12	-89.43	1,128 (a)	F	unconfirmed Bryde's-like whale	no photos or notation of rostral ridges	
MME 11756	SE4038, SWF-BE- 8876-B	11/25/88	Honeymoon Island, off Clearwater, FL	28.08	-82.83	693	F	Bryde's-like whale	photos; Edds <i>et al.</i> 1993	Jefferson 1995
STR 339		4/2/65	Panacea, FL	30.03	-84.37	1,158	n/a	Bryde's-like whale	photos; Rice 1965	Lowery 1974; Mead 1977; Shane and Schmidly 1976; Schmidly 1981
STR 1923=STR 2507		1/11/75	West Bay Region Near Venice/ near Tiger Pass, LA	29.12	-89.40	841	M	Bryde's-like whale	visual observation of ridges; Shane and Schmidly 1976	Mead 1977; Schmidly 1981;
USNM 504074	BAP001, CSLP7674	5/29/74	Tarpon Springs, Anclote Key, FL	28.15	-82.77	1,000	M	Bryde's -like whale	photos; Mead 1977	Gunter and Overstreet 1974; Schmidly 1981; Jefferson 1995
UF33536	USNM 593536; MMPL0906; SER09-0394	10/4/09	Tampa Bay, FL	27.91	-82.43	1,265 (a)	F	verified GOMx Bryde's-like whale	genetics; Rosel and Wilcox 2014	
USNM 593537	FLGM11020 6-32; SER06-575	11/2/06	Walton County, FL	30.37	-86.35	470 (e)	F	verified GOMx Bryde's-like whale	genetics; Rosel and Wilcox 2014	
0521Be	SER05-767	3/28/05	Southwest Pass, LA	28.99	-89.38	914 (a)	F	verified GOMx Bryde's-like whale	genetics; Rosel and Wilcox 2014	
RKB-1403	SE4022	8/20/88	Panama City, FL	30.08	-85.64	450 (p)	unk	Bryde's-like whale	baleen, throat groove location, size; R. K. Bonde unpublished	Jefferson 1995
LSUMZ 033431	LSUMZ033 43	2/28/82	near Southwest Pass, LA	29.07	-89.29	n/a	n/a	baleen whale	no photos or notation of rostral ridges	Jefferson 1995
MCT20120326	SER12-0585	3/18/12	North edge of Chandeleur Islands chain, LA	29.98	-88.83	701 (p)	n/a	verified GOMx Bryde's-like whale	genetics; present study	



SMM20121101	SER12-0771	10/25/12	Lonesome Bayou, SE corner of Breton Sound, LA	29.20	-89.06	780 (p)	M	verified GOMx Bryde's-like whale	genetics; present study	
44DISL091616	SER16- 00537	9/15/16	25 miles offshore Louisiana, trawl	n/a	n/a	n/a	n/a	baleen whale	bone only	
USNM 594665	FMMSN190 8, SER19- 00187	1/29/19	Everglades National Park, FL	25.03	-81.02	1,126 (a)	M	verified GOMx Bryde's-like whale	genetics; present study	holotype
<b>Atlantic</b>										
USNM 239307		3/18/192 3	Walnut Point, VA	37.98	-76.47	801-803	M	Bryde's-like whale	photos	Mead 1977
USNM 572922	WAM 587	3/13/03	Carolina Beach, NC	34.07	-77.88	1,105 (a)	M	verified GOMx Bryde's-like whale	genetics; Rosel and Wilcox 2014	
MME 8115	SC-92-1, SE6591	1/24/92	Ash Island, St. Helena Sound, SC	32.5	-80.45	790 (a)	F	verified GOMx Bryde's-like whale	genetics; Rosel and Wilcox 2014	
MME 93	GA8301050 1	1/5/83	Ossabaw Island, GA	31.74	-81.11	660 (e)	n/a	Bryde's-like whale	Stranding record indicates rostral ridges present	
MME 11032	SE8345, GA8301050 1	9/18/93	Ossabaw Island, GA	31.87	-81.13	510 (a)	n/a	unconfirmed Bryde's-like whale	Highly decomposed. No photos or notation of rostral ridges	
SEAN 1209		11/6/76	Fort Pierce, FL	27.47	-80.33	559	F	Bryde's-like whale	photos with stranding record	Schmidly 1981
USNM 504768	SEAN3080, SE0028	3/14/78	Fort George Island, FL	30.42	-81.41	869 (a)	M	Bryde's-like whale	photos; Leatherwood and Reeves 1983	Schmidly 1981,
MME 3360		8/30/87	Amelia Island, FL	30.57	-81.45	975	n/a	unconfirmed Bryde's-like unconfirmed Bryde's-like whale	No photos, animal swam away	
SEAN 3212	SE0064, HNN-884,	4/30/78	"Orange Canal between Ogeechee river and Rockfish creek"	31.92	-81.23	950-953	M	unconfirmed Bryde's-like whale	No photos or notation of rostral ridges	Schmidly 1981



Figure 1

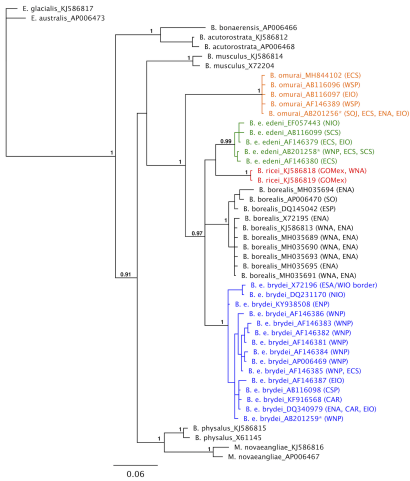


Figure 2

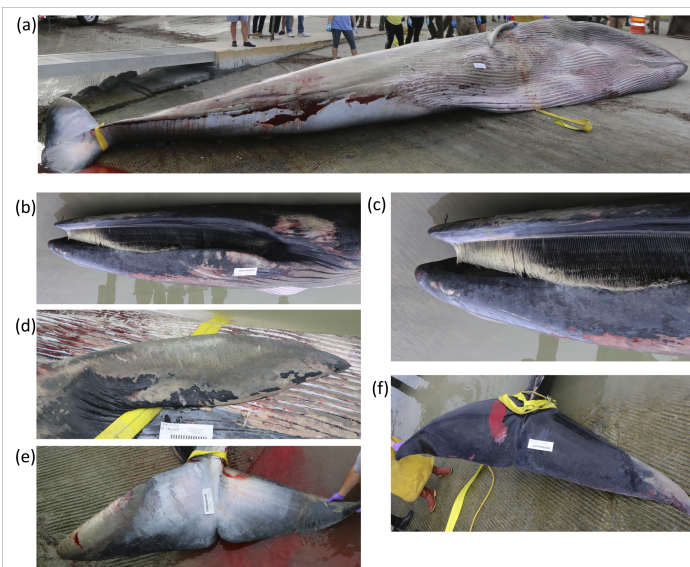


Figure 3

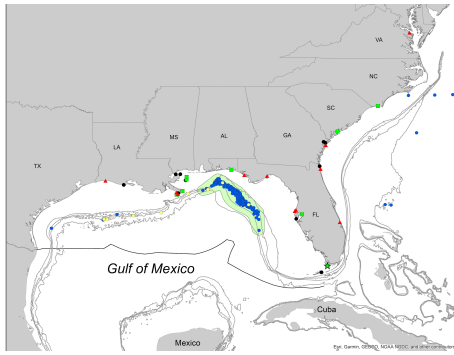


Figure 4



Figure 5



Figure 6

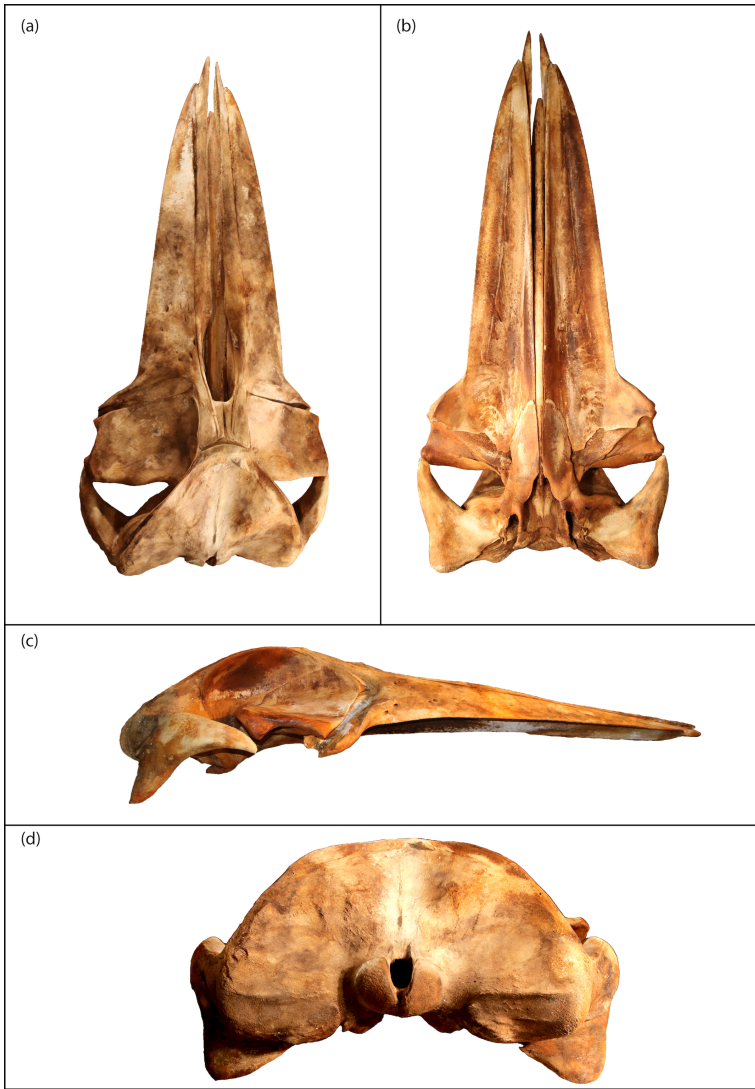


Figure 7



Figure 8