Marine Mammal Science

OPINION

Rice's Whale: Considerations for Identifying New Cetacean Species

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ABSTRACT

Rice's whale (*Balaenoptera ricei*), recently classified as a species distinct from Bryde's whales, exemplifies the challenges in cetacean taxonomy arising from limited morphological divergence and an overreliance on restricted genetic datasets. Darwin's principle, that species represent "dominant varieties" within a continuum, underscores the inherent subjectivity in such taxonomic judgments. Genetic analyses based on mitochondrial DNA (mtDNA) haplotypes identify Rice's whale as a monophyletic lineage, yet its pronounced genetic homogeneity may reflect recent demographic bottlenecks, possibly caused by historical whaling, rather than deep evolutionary isolation. Morphological differentiation, although subtle, includes cranial features primarily involving nasal bones. Ecologically, Rice's whales occupy a restricted range in the northeastern Gulf of Mexico, potentially representing a relict population that was historically more widespread before commercial whaling. Comparative cases, such as North Atlantic right whales and northern elephant seals, illustrate how severe population reductions can rapidly produce distinct genetic profiles. The issue is not the use of genetic evidence itself but its interpretation: genetic diagnosability, particularly when based on limited mtDNA data, is not equivalent to speciation and may simply reflect restricted gene flow or recent isolation without reproductive or ecological divergence. Recognizing Rice's whale as a species thus highlights the tension between taxonomy based primarily on molecular diagnosability and a more integrative approach, emphasizing the need for multiple, concordant lines of evidence before assigning full species status.

1 | Introduction

Charles Darwin regarded the distinction between species and varieties as often subjective (Darwin 1859). In *On the Origin of Species*, he observed that no single definition of species has satisfied all naturalists, yet each naturalist intuitively understands the meaning of the term. He considered species designations somewhat arbitrary, viewing species essentially as "well-marked varieties," forms (groups of organisms) exhibiting stable, clear, and readily recognizable differences distinguished primarily for convenience. Darwin thus characterized species not as fixed entities but as segments along a continuum of variation and divergence within populations containing multiple varieties, with the term "species" typically applied to the most common, widely distributed, or dominant forms.

In contrast, varieties represent less divergent, less abundant, and more geographically restricted forms within these variable populations, emphasizing common descent without precise boundaries separating varieties from species. He viewed species as dynamic populations continually changing, where a variety today might become a species tomorrow through divergence and the loss of intermediate forms. Darwin cautioned that, without clear consensus or criteria, arguing whether a form is a species or a variety is to "vainly beat the air" (Darwin 1859). This Darwinian viewpoint underscores the continuum of divergence and inherent subjectivity in taxonomic judgments. With this perspective in mind, I examine the taxonomic status of Rice's whale (*Balaenoptera ricei*), endemic to the Gulf of Mexico, to determine whether its recent designation as a distinct species is justified in light of Darwin's principles and modern evolutionary science (Avise 2000; Isaac et al. 2004). I selected Rice's whale as a recent case study to guide future cetacean species designations.

Rice's whale had long been considered a population of Bryde's whales (*Balaenoptera edeni/brydei*) in the Gulf of Mexico, following its "rediscovery" in the 1990s during surveys of marine mammal, seabird, and sea turtle distribution and abundance, sponsored by the U.S. Department of the Interior, to support environmental assessments before oil and gas development on the continental slope (Davis et al. 1999). "Bryde's-like" whales constitute a complex of medium-sized, tropical rorquals with at least two recognized forms: the larger, pelagic Bryde's whale (often termed *B. edeni brydei*) and the smaller, coastal Eden's whale (*B. edeni edeni*). Taxonomic clarity within this group has historically been elusive. Notably, Japanese researchers discovered Omura's whale (*Balaenoptera omurai*), initially confused with Bryde's whales, and formally described it as a new species based on distinct skull morphology and mitochondrial DNA (mtDNA), prompting them to suggest that Bryde's and Eden's whales represent separate species (Wada et al. 2003). Subsequent studies of Bryde's whales reinforced the existence of divergent genetic lineages; for instance, significant genetic diagnosability was documented between the coastal (Indian and Northwest Pacific Oceans) and offshore populations (Kershaw et al. 2013). However, the authors stopped short of recommending formal taxonomic designation, instead proposing that each genetically differentiated population be treated as an independent conservation unit for management purposes.

Until recently, the Gulf of Mexico population of "Bryde's-like" whales was managed as an endangered subpopulation or subspecies. However, in 2021, Rosel et al. (2021) formally described this population in accordance with the International Code of Zoological Nomenclature and proposed the species name *B. ricei*. This designation culminated over a decade of research following the initial genetic evidence of divergence (Rosel and Wilcox 2014). With fewer than 100 individuals (perhaps only ~50) remaining and a year-round habitat confined almost entirely to the northeastern Gulf of Mexico, the Rice's whale instantly became one of the world's most endangered species of large whales. Outwardly, Rice's whales are virtually identical to Bryde's whales, sharing characteristics like a sleek dark-gray body and the three prominent parallel ridges on the rostrum (front of the head) that distinguish Bryde's/Eden's and Omura's whales from other rorquals (Figure 1). This superficial similarity underscores Darwin's point that morphological continuity can blur the lines between species and variety. To evaluate Rice's whale's taxonomic status, I consider the genetic, morphological, reproductive, ecological, and historical evidence of differentiation against Darwin's caution about taxonomic subjectivity.

2 | Genetic Evidence and Evolutionary Divergence

Genetic data have been key in identifying Rice's whale as a separate lineage. mtDNA sequences from Gulf of Mexico whales show divergence from those of all other Bryde's and Eden's whales (Rosel and Wilcox 2014; Rosel et al. 2021). The taxonomic framework used to support this designation followed the philosophy advanced by Taylor et al. (2017), which established a genetic threshold for species diagnosability. In an analysis of mtDNA control region sequences, Rice's whale haplotypes were found to be unique and as divergent from other Bryde's whale varieties as those lineages are from each other (Rosel and Wilcox 2014). Specifically, researchers reported 25–26 fixed nucleotide differences in a short segment of the mtDNA between the Gulf of Mexico population and both the Bryde's whale and the Eden's whale, as well as relative to the closely related sei whale (*Balaenoptera borealis*) (Rosel and Wilcox 2014). This degree of sequence divergence equals or exceeds differences observed among other long-recognized whale species, suggesting that the Gulf population underwent allopatric speciation because of prolonged evolutionary isolation (Avise 2000; Isaac et al. 2004).

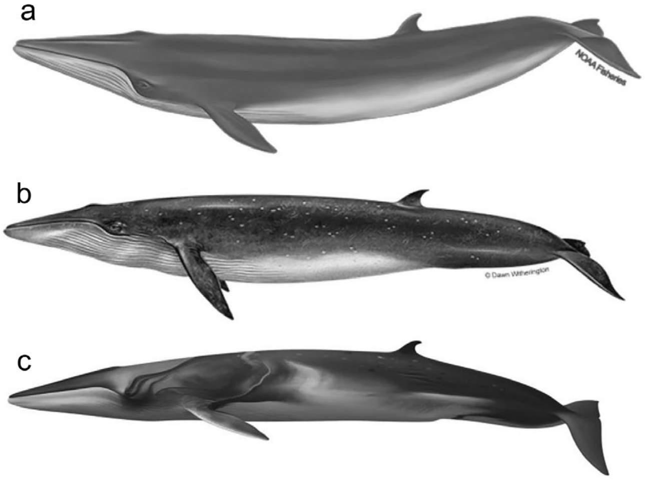

FIGURE 1 | Artistic renderings of (a) Rice's whale, (b) Bryde's whale, and (c) Omura's whale. Images (a) and (b) are from the National Oceanic and Atmospheric Administration (NOAA) Fisheries website (https://www.fisheries.noaa.gov/species/).

Expanding the genetic perspective, a 2021 study increased the sample size to 36 Gulf of Mexico whales, confirming their membership in a single maternal lineage distinct from other known Bryde's-like whales (Rosel et al. 2021). Microsatellite DNA markers and nuclear gene sequences provide additional insight: the Gulf whales exhibit extremely low genetic diversity (likely reflecting a small, isolated population) but also possess specific allele patterns not seen elsewhere (Rosel and Wilcox 2014). As is common among baleen whales, many nuclear gene variants are shared across *Balaenoptera* species because of their recent common ancestry and slow evolutionary rates. Phylogenetic analyses combining multiple genes nevertheless place the Gulf of Mexico whales on a distinct branch relative to *B. edeni edeni* and *B. edeni brydei*, with mitochondrial data indicating that Rice's whale forms a reciprocally monophyletic lineage consistent with recognition as a distinct evolutionary unit under the phylogenetic species concept. However, additional genome-wide analyses are needed to confirm this relationship (Rosel and Wilcox 2014; Rosel et al. 2021; Lin et al. 2025).

3 | Limitations of the Genetic Evidence

It is essential to recognize the limitations of genetic diagnosability when based on restricted datasets. A DNA-based identification system functions effectively only when species or varieties are represented by sufficiently large sample sizes that capture their true genetic variation. An incomplete or sparse database will merely allow users to determine if a given sequence differs from those already stored. Such a result neither definitively identifies the specimen nor necessarily indicates a new species. However, the fundamental goal of taxonomy is not merely to identify species but to delineate them clearly from closely related varieties, a process that remains challenging and continually refined as new genetic, morphological, and ecological data become available. Genetic diagnosability, especially in mtDNA, is not equivalent to speciation; it may simply reflect restricted gene flow or recent isolation without the emergence of reproductive incompatibilities or ecological differentiation (Hillis 2019).

The genetic diagnosability of Rice's whale can be interpreted by considering both ancient and recent demographic events. Historical records indicate that commercial whaling in the Gulf of Mexico during the 18th and 19th centuries may have reduced populations of Bryde's-like whales, potentially creating a genetic bottleneck (Reeves et al. 2011). Whaling logbooks from that era document numerous encounters with "finback" whales, likely Bryde's or closely related *Balaenoptera* species, suggesting that Rice's whales represent a relict population from a once more widespread lineage. mtDNA, being haploid and maternally inherited, can reach fixation rapidly in small populations, which may exaggerate the appearance of divergence even when long-term lineage independence has not occurred. Thus, demographic history may influence patterns of diagnosability without altering true phylogenetic relationships. The observed mtDNA divergence might reflect an ancient lineage separation or the outcome of historical demographic events, such as genetic drift following a population reduction (Avise 2000). If the population was reduced, it may have left only a few survivors carrying a single maternal lineage, creating a pseudo-founder effect that fixed a single mtDNA haplotype and inflated the apparent genetic distinctiveness, highlighting the limitations of relying solely on mitochondrial data rather than genetic evidence as a whole. Indeed, Rice's whales exhibit nearly homogeneous mtDNA, with only two haplotypes identified in the mtDNA control region and no variation detected in Cytochrome b (*cytb*) or Cytochrome oxidase subunit 1 (*cox1*) sequences, suggesting synonymous (neutral) evolutionary changes without adaptive divergence (Avise 2000; Rosel and Wilcox 2014; Rosel et al. 2021). Nuclear DNA differentiation is less pronounced, with many loci showing no fixed differences, which may indicate a recent demographic event, possibly dating as recently as the 1800s.

Thus, it is plausible that an originally unremarkable Bryde's whale population in the Gulf of Mexico became genetically distinctive in mtDNA alone through stochastic processes associated with a genetic bottleneck, such as 19th-century commercial whaling, although this remains uncertain without corroboration from whole-genome data. Even relatively brief isolation, coupled with a small population size, can produce pronounced mtDNA differentiation (Avise 2000). Similar bottlenecks occurred in North Atlantic right whales (*Eubalaena glacialis*), which were reduced to fewer than 100 individuals by intensive whaling, leading to low mtDNA diversity and haplotype fixation (Malik et al. 2000; Rosenbaum et al. 2000; Schaeff et al. 1997), and northern elephant seals (*Mirounga angustirostris*), whose extreme genetic depletion resulted from hunting that left possibly 20–30 survivors (Hoelzel et al. 1993). These cases illustrate how severe bottlenecks can rapidly reduce mitochondrial diversity and fix a limited number of haplotypes, producing superficially distinct genetic profiles through drift rather than reflecting deep evolutionary divergence. As a result, even formal genetic guidelines acknowledge that small effective population sizes can generate fully sorted genetic differences without fulfilling the biological criteria intended for subspecies or species designation (Taylor et al. 2017).

For Rice's whales, an ancient origin and a recent bottleneck are not mutually exclusive; a combination of long-term isolation and severe genetic drift may best explain their current genetic profile. Because neutral genetic differences can arise randomly through drift, species recognition based solely on such divergence must also demonstrate genealogical exclusivity; that is, clear evidence that the populations form independent, nonoverlapping lineages across multiple genes. Apparent drift-based divergence in small or bottlenecked populations may be transient and reversible through later gene flow. However, unlike systems where drift has produced genome-wide reciprocal monophyly and strong species-delimitation support (e.g., Black et al. 2024), no comparable nuclear evidence currently demonstrates that Rice's whale represents an irreversibly diverged lineage. Integrative taxonomy requires genetic, morphological, and ecological congruence before conferring full species rank (Dayrat 2005). Regardless of the precise mechanism, the markedly reduced genetic diversity observed in this population has important implications for its taxonomic classification. Rice's whale exemplifies how mtDNA lineages in endangered populations may reflect demographic events as strongly as deeper evolutionary history.

While the observed genetic divergence in Rice's whale aligns with recognized species-level differences in some taxa, using numeric genetic thresholds for species delineation is problematic. For example, Taylor et al. (2017) proposed a $>2\%$ net mtDNA divergence as a criterion for cetacean species delimitation, but such arbitrary cutoffs can mislead classification. An isolated population might exceed this threshold via genetic drift without having undergone prolonged independent evolution through natural selection and genealogical exclusivity. No single genetic threshold universally applies to intraspecific differentiation, as appropriate cutoffs vary widely depending on the evolutionary rates of genetic markers and the taxonomic group considered (Bickford et al. 2007). Threshold calibration typically involves empirical determination from multiple specimens per species, calculating pairwise genetic distances, and comparing these distances against existing morphological or ecological species boundaries (Lefébure et al. 2006). However, applying these thresholds across taxa (e.g., birds, amphibians, and crustaceans) can lead to inconsistent taxonomic decisions, resulting in either over-splitting or under-splitting. Circular reasoning "taxonomic circle" is a critical concern in which existing taxonomy defines the thresholds later used to delimit species, thereby reinforcing initial assumptions and creating confirmation bias. Because such genetic thresholds are the very criteria used to justify species status in other cases, applying them here risks a circular justification for elevating Rice's whale to species rank (Rosel and Wilcox 2014; Taylor et al. 2017).

Genetic thresholds should serve as initial hypotheses that are validated through independent morphological, reproductive, ecological, or behavioral evidence. Excessive reliance on universal genetic thresholds risks prematurely elevating incipient varieties within closely related groups to the status of species, obscuring the evolutionary processes, both adaptive and non-adaptive, that drive divergence and ultimately give rise to stable, independently evolving lineages. Therefore, genetic diagnosability alone does not satisfy strict biological species criteria unless it is coupled with evidence of reproductive isolation or meaningful morphological and ecological differentiation (Dayrat 2005; Chambers and Hillis 2020; Sukumaran et al. 2021). A robust justification for a separate species designation requires additional, comprehensive genomic analyses demonstrating consistent divergence across multiple unlinked nuclear loci, which clearly exceeds the scope of the current data for Rice's whale (Coyne and Orr 2004; Lin et al. 2025).

Building on this concern, species delimitation in recent years has advanced well beyond the use of mitochondrial thresholds. Modern coalescent-based approaches, such as those reviewed by Coyne and Orr (2004) and formalized under the unified species concept by de Queiroz (2007), emphasize that species are best viewed as separately evolving metapopulation lineages, with different operational criteria (diagnosability, reproductive isolation, monophyly, ecological distinctness) serving as lines of supporting evidence. More recent contributions have highlighted both the power and pitfalls of these approaches. Burbrink and Ruane (2021) and Burbrink et al. (2024) demonstrate how genomic-scale data and species delimitation models can identify cryptic lineages but also risk oversplitting if demographic history is not accounted for, while Hillis et al. (2021) caution that such analyses must be interpreted within an integrative framework that includes morphology and ecology. This literature underscores why a heavy reliance on mtDNA is problematic for Rice's whale and why a broader integrative phylogenetic approach that incorporates nuclear, morphological, and ecological data remains essential and has not yet been satisfactorily demonstrated.

4 | Morphological and Ecological Evidence

4.1 | Morphology

Despite their similar external appearance, Rice's whales exhibit subtle skeletal differences that distinguish them from their relatives, Bryde's and Eden's whales. Externally, traits overlap extensively among these taxa, and no suite of gross external features has yet been demonstrated to distinguish Rice's whale with statistical confidence (Wada et al. 2003; Yamada et al. 2008). The most diagnostic traits are found in the skull, particularly the nasal bones and surrounding anatomy (Rosel et al. 2021). In Rice's whale, the nasal bones taper laterally with smooth margins, and the frontal bones extend back around the nasals, producing a broader posterior gap than in Bryde's or Eden's whales (Figure 2; Rosel et al. 2021). In contrast, the posterior edges of the nasal bones in Bryde's whales (*sensu stricto*) are relatively straight and closely aligned, with the frontal bones not intruding as far between them. Eden's whale (the smaller coastal form) has its own skull distinctions (e.g., a more triangular nasal bone shape and different frontal bone exposure) (Rosel et al. 2021). These cranial characters were identified through direct side-by-side comparisons of the complete Rice's whale skull recovered from a 2019 Florida stranding (holotype specimen USNM 594665) and a 2003 North Carolina specimen (USNM 572922), both representing the Gulf of Mexico lineage, with multiple Bryde's whale skulls (Rosel et al. 2021). An incomplete skull collected in 1954 from Louisiana (LSUMZ 17027) was examined only for genetic data (Rosel et al. 2021).

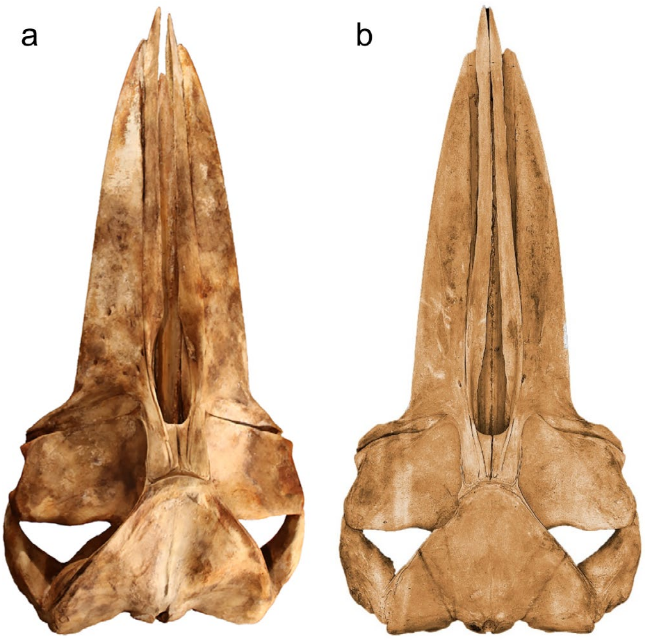

FIGURE 2 | Skulls from (a) Rice's whale (Holotype Specimen USNM 594665) and (b) Bryde's whale. Image (a) from Rosel et al. (2021) and (b) from Yamada et al. (2008).

The osteological distinctions are subtle and documented from only two complete skulls, such that reliable diagnosis presently requires standardized morphometric analysis; with this sample size, effect sizes and statistical significance cannot yet be assessed (Rosel et al. 2021). Although these cranial features appear consistent, the small sample size warrants caution because it is insufficient to rule out individual or regional variation. It therefore remains uncertain whether these minor traits are functionally significant or reflect adaptive differences rather than neutral variation. As Darwin noted in his discussion of the mutual affinities of organic beings, "A classification founded on any single character, however important that might be, has always failed, for no part of the organization is invariably constant" (Darwin 1859). To avoid the risk of creating *junior synonyms*, species designations should be based on multiple diagnostic characters and more than a few specimens, particularly in widely distributed and variable taxa such as Bryde's-like whales.

Historically, morphological taxonomists, notably Ernst Mayr and George Gaylord Simpson, adhered strictly to the Biological Species Concept (BSC), emphasizing reproductive isolation and requiring consistent morphological differences across multiple characters, often both structural and functional, before recognizing a new mammalian species (Mayr 1942; Simpson 1961). They argued that isolated morphological traits or subtle variations could represent intraspecific polymorphism, geographic variants, or subspecies rather than distinct species. Consequently, declaring a new species under their criteria necessitated robust and reproducible morphological and functional distinctions indicative of true evolutionary divergence and adaptive differentiation, rather than merely superficial or isolated variations (Mayr 1969; Simpson 1951).

From a Darwinian perspective, it is unlikely that the minor differences in the skull morphology of Rice's whale influence physiological function, ecological performance, or reproductive success. From a neutral evolutionary perspective, an equally plausible explanation is that these subtle skull differences represent random genetic drift without genealogical exclusivity or the consequence of historical demographic events, such as population bottlenecks or founder effects (Avise 2000; Coyne and Orr 2004). Other than the slight differences in skull morphology, there are no noticeable external differences between Rice's and other Bryde's-like whales (Rosel et al. 2021). Critics might question whether the observed nasal bone differences are truly sufficient to warrant species status rather than merely a regional varietal distinction. Externally, the whales are so similar that only genetic testing or detailed inspection of skulls can reliably distinguish them, raising a fundamental question: if two organisms appear and behave similarly, should they be classified as varieties of the same species?

4.2 | Ecology and Behavior

The ecology of Rice's whale is unique primarily because it is the only rorqual endemic to the Gulf of Mexico, and even then, it is mainly restricted to a small range along the continental slope of the northeastern Gulf in waters approximately 150–400 m deep. These facts align with its genetic isolation. Historical evidence suggests that Rice's whales may have been more widely distributed throughout the Gulf, indicating they may represent a remnant of a formerly broader lineage (Reeves et al. 2011). This suggests their limited distribution likely reflects a relic population resulting from historical declines, possibly because of whaling.

However, *ecologically*, Rice's whale plays a role very similar to that of Bryde's whales elsewhere as a medium-sized rorqual feeding in warm-temperate waters. It does not fill a novel niche so much as the same niche in a different location. In Darwin's view, a “well-marked variety” might simply be a local adaptation or isolated population of a species unless it shows fundamental ecological or behavioral divergence. The guidelines of Taylor et al. (2017) mention behavioral or ecological concordance only as a supplemental check, not as a prerequisite. Rice's whales have a distinct call type, but regional dialects are common in whales and do not, on their own, imply species-level separation (many populations of the same species have unique calls) (Soldevilla et al. 2022). Here, the Darwinian perspective urges restraint: this variety (Rice's whale) might not have diverged in any major ecological function from the parent species.

5 | The Bryde's Whale Complex in Context

Understanding the taxonomic status of Rice's whale also requires comparison with its closest relatives and evaluation of analogous taxonomic cases in other whale species.

5.1 | Bryde's vs. Eden's Whales

The larger offshore form (Bryde's whale) and the smaller coastal form (Eden's whale) have long perplexed taxonomists. Initially described more than a century ago, these whales were often treated as a single species, differing only in size or ecotype. Modern studies show clear genetic and morphological divergence between them, and some experts now recognize them as two species, or at least closely related subspecies (Wada et al. 2003; Kershaw et al. 2013). Notably, Bryde's and Eden's whales differ consistently in adult size, skull proportions, and baleen plate counts. However, considerable taxonomic uncertainty remains surrounding the name *B. brydei*, particularly in the Atlantic and Caribbean. Luksenburg et al. (2015) demonstrated that the offshore form *B. e. brydei*, referred to as the Aruban whale, occurs in the southern Caribbean, whereas Rosel and Wilcox (2014) identified a distinct Gulf of Mexico lineage, now recognized as Rice's whale. mtDNA analyses confirm that the Aruban whales are not Rice's whale; they cluster within the offshore *B. e. brydei* clade, whereas Rice's whale forms a reciprocally monophyletic Gulf of Mexico lineage (Luksenburg et al. 2015; Rosel et al. 2021). These findings underscore that multiple Bryde's-like lineages coexist in the Atlantic, complicating species delimitation and highlighting the need for integrative taxonomic frameworks. For example, off South Africa, there are distinct offshore and inshore Bryde's whale populations, but it remains unclear which corresponds to *B. brydei* in a global framework and how the inshore population relates to other Bryde's-like whales. This ambiguity reflects the legacy of holotype designations and traditional taxonomy, which continue to impede clear species recognition.

If the scientific community moves toward recognizing *B. brydei* and *B. edeni* as separate species, then the Gulf of Mexico population would add a third branch to this Bryde's-like group. In fact, the mtDNA genetic divergence of Rice's whale from either Bryde's or Eden's whales is comparable to or greater than the divergence observed between those two forms (Rosel and Wilcox 2014; Taylor et al. 2017). Thus, if Bryde's and Eden's whales are deemed separate species, Rice's whale logically qualifies as one as well. On the other hand, if a more conservative approach were adopted and Bryde's and Eden's were treated as a single species with regional varieties, then Rice's whale might be classified as another variety under that broader species. This contrast illustrates the subjective judgment involved in species delineation: the same evidence can support either multiple species or a single species with regional varieties, depending on one's taxonomic philosophy (de Queiroz 2007; Dayrat 2005; Sukumaran and Knowles 2017; Zachos 2018b; Burbrink and Ruane 2021). Notably, some recently proposed standards favor splitting any diagnosable lineages for consistency (Taylor et al. 2017), whereas more conservative approaches emphasize the potential for such divergent forms to remain varieties within a single species.

5.2 | Omura's Whale

Omura's whale provides a precedent for recognizing cryptic species (i.e., genetically divergent with minimal external morphological differentiation; Bickford et al. 2007) within this whale group. It was initially considered a dwarf or aberrant form of Bryde's whale in the Indo-Pacific until morphological and genetic analyses revealed distinctive cranial features and mtDNA divergence of 5%–8% from Bryde's whales, well above Taylor et al.'s 2% guideline (Wada et al. 2003; Taylor et al. 2017). This evidence was sufficiently compelling to formally designate Omura's whale as a separate species in 2003. Omura's whale appears to represent an ancient lineage, genetically distinct from Bryde's/Eden's whales despite superficial external similarities (Figure 1c). Rice's whale is a small, geographically isolated whale restricted to the northeastern Gulf of Mexico, whereas Omura's whale, although morphologically and genetically distinct, occurs broadly across the Indo-Pacific and has also been reported from the Atlantic (Wada et al. 2003; Yamada et al. 2008; Cerchio et al. 2019; Rosel et al. 2021).

Unlike Omura's whale, which shows more pronounced morphological distinctions such as smaller adult size, distinct coloration patterns, and clear genetic differentiation supported by both mitochondrial and nuclear DNA, Rice's whale appears externally nearly indistinguishable from Bryde's/Eden's whales, making morphological differentiation less evident to casual observers (Wada et al. 2003; Sasaki et al. 2005; Yamada et al. 2008; Cerchio et al. 2015, 2019). Nevertheless, from mtDNA and osteological perspectives, the divergence of Rice's whale is comparable to that of Omura's whale. Recognizing Omura's whale as a separate species established a precedent that the Bryde's whale complex contains multiple species rather than mere varieties. However, Omura's whale was validated through multiple lines of evidence and is more broadly distributed, not solely based on genetic divergence from phylogenetic analyses. From a Darwinian perspective, though, Omura's whale still lies on the edge of species designation, illustrating the difficulty of distinguishing between well-marked varieties and true species within a continuum of divergence. Its designation involved thorough morphological examinations of numerous specimens, including consistent cranial and skeletal characteristics distinct from related taxa (Wada et al. 2003; Sasaki et al. 2005; Yamada et al. 2008; Cerchio et al. 2015). This example underscores the necessity for careful evaluation to prevent unwarranted taxonomic splits and associated inflation (Isaac et al. 2004; Avise 2000; Coyne and Orr 2004).

5.3 | Pygmy Blue Whale

The blue whale (*Balaenoptera musculus*) has a recognized subspecies called the pygmy blue whale (*B. m. brevicauda*), found in the Indian and southern Pacific Oceans. Pygmy blue whales differ from "true" blue whales in body size (maximum ~24 m vs. 30 m), certain skeletal features (e.g., relatively shorter tail length), and exhibit genetic differentiation. However, they are not classified as a separate species but remain a subspecies, illustrating taxonomic conservatism. This classification hinges on the fact that pygmy blue whales intergrade with other blue whale populations (i.e., they lack absolute reproductive isolation) and exhibit lower genetic divergence, indicating some ongoing gene flow (Ichihara 1966; LeDuc et al. 2007; Attard et al. 2012). In a Darwinian sense, the pygmy blue whale represents a variety or race of the blue whale species that has not yet diverged irreversibly. By comparison, Rice's whales are allopatric, with no documented interbreeding with other Bryde's-like whale populations. Additionally, the genetic divergence between Rice's and Bryde's/Eden's whales is greater: the entire mitochondrial lineage of Rice's whale is distinct, whereas pygmy blue whales share some mtDNA lineages with other blue whales. This comparison underscores that Rice's whale is more clearly justified as a separate species than some subspecies-level cases, such as the pygmy blue whale, because of its greater degree of isolation and diagnostic differences. Nevertheless, the pygmy blue whale exemplifies taxonomic conservatism; despite its distinct traits, it remains a subspecies because of some gene flow and continuity with other blue whale populations. By similar logic, one could argue that Rice's whale, despite its greater isolation, should be regarded as an isolated variety of Bryde's whale rather than elevated to full species status. However, whether its distinctiveness reflects long-term adaptive divergence over an extended evolutionary timespan, or a recent bottleneck remains uncertain, as genealogical exclusivity across multiple loci has not been demonstrated.

5.4 | Killer Whale

A long-standing debate in marine mammalogy concerns the taxonomic status of the killer whale (*Orcinus orca*). Globally, killer whales are recognized as a single, cosmopolitan species, although multiple ecotypes have been described: for example, fish-eating "resident" and marine-mammal-eating "Bigg's/transient" ecotypes in the North Pacific, and several distinct forms in Antarctic waters. These ecotypes differ in diet, social structure, vocal dialects, and some morphological traits, and early mitogenome work revealed deep lineage divergence, leading Morin et al. (2010) to propose that multiple species might be grouped under one name. Subsequent nuclear analyses showed comparable population structure (Parsons et al. 2013), and expanded genomic datasets provided a more nuanced picture: genome-wide differentiation among ecotypes together with signatures of historical gene flow, admixture, and incomplete lineage sorting (Morin et al. 2015; Foote et al. 2016, 2019). Collectively, these results indicate a reticulate evolutionary history at a global scale, in which most populations have undergone substantial ecological and genetic divergence without uniformly achieving complete reproductive isolation.

Within this global context, regional exceptions now appear. Using an explicitly integrative framework (genomic, morphological, ecological, and behavioral/acoustic evidence), Morin et al. (2024) argued that the eastern North Pacific resident and Bigg's ecotypes meet species-level criteria, reflecting long-term evolutionary independence in that region. At the same time, genome-wide analyses of runs of homozygosity show that demographic histories, bottlenecks, and admixture vary by population and can shape genetic distinctiveness without necessarily completing speciation (Foote et al. 2021). Accordingly, the weight of evidence supports a scale-dependent view: a globally reticulate complex with some lineages (e.g., eastern North Pacific residents and Bigg's) meeting species-level standards under an integrative test, while many others remain divergent ecotypes or incipient lineages pending concordant evidence across data classes.

Recent studies have identified additional ecological and social substructure within North Pacific killer whales, including inner- and outer-coast transient subpopulations and a potential offshore/oceanic form (McInnes et al. 2024, 2025). These patterns currently reflect behavioral and ecological partitioning rather than fixed morphological or genome-wide differentiation, and no evidence yet indicates genealogical exclusivity or reproductive isolation among these units (McInnes et al. 2024, 2025). Consequently, such variation is best interpreted as incipient varieties or stable ecotypes within a single, polymorphic species complex rather than distinct evolutionary lineages.

Taxonomic proposals to formalize portions of killer whale diversity (e.g., *Orcinus ater* and *O. rectipinnis*) have not been adopted by the Society for Marine Mammalogy's Committee on Taxonomy, which maintains a single-species classification pending stronger integrative evidence and clearly separate lineages based on nuclear DNA (Committee on Taxonomy 2024). This conservative stance aligns with the global genomic record, which reveals a reticulate evolutionary history shaped by episodic admixture, and with current best practice that species recognition should rest on concordance across genomic, morphological, ecological, and reproductive evidence rather than mitochondrial diagnosability or ecological segregation alone. Within this framework, the eastern North Pacific resident and Bigg's lineages may stand out as regionally completed examples of speciation, exhibiting genealogical exclusivity supported by concordant genomic, morphological, ecological, and behavioral evidence at sample sizes sufficient for statistical diagnosis. Together, these results show how killer whales exemplify the rigorous, multi-line approach that defines modern integrative taxonomy, where multiple, independent lines of evidence converge to support species recognition of regional varieties. This approach establishes a standard of evidentiary robustness and analytical breadth not yet achieved in the case of Rice's whale, whose designation as a distinct species was based primarily on mitochondrial diagnosability and limited cranial morphology.

5.5 | Integrative Evaluation of Species Criteria

Within the framework proposed by Taylor et al. (2017), which identifies > 2% net mtDNA divergence as indicative of species-level separation, comparisons with blue and killer whales underscore the limits of this threshold. The pygmy blue whale shows only 0.5%–1.2% divergence from "true" blue whales and remains a subspecies because gene flow persists (LeDuc et al. 2007; Attard et al. 2012), whereas Rice's whale exhibits 1.8%–2.9% divergence from Bryde's and Eden's whales (Rosel and Wilcox 2014; Lin et al. 2025) but lacks corroborating nuclear, morphological, or ecological differentiation. Similarly, killer whale ecotypes diverge by 0.7%–3.0% in mtDNA yet are treated as one species because of incomplete genomic and reproductive isolation (Morin et al. 2010). These examples demonstrate that genetic thresholds alone are insufficient for species designation without integrative supporting evidence.

6 | Macroevolutionary and Microevolutionary Evidence for Species Designation of Rice's Whale

Taken together, the available data indicate that Rice's whale displays a combination of macroevolutionary and microevolutionary characteristics consistent with partial lineage differentiation but insufficient evidence of complete species-level divergence. Macroevolutionary evidence includes mtDNA analyses showing that Gulf of Mexico whales form a distinct haplotype cluster, with divergence from Bryde's and Eden's whales comparable to that among recognized species-level splits (Rosel and Wilcox 2014). However, nuclear genetic data, which provide a broader evolutionary signal, reveal extremely low diversity and extensive allele sharing with other *Balaenoptera* species, offering little evidence of long-term reproductive or genealogical isolation (Rosel et al. 2021). Although the population is geographically restricted and genetically diagnosable, these patterns may reflect stochastic drift or founder effects following a demographic bottleneck rather than sustained evolutionary independence (Avise 2000; Hoelzel et al. 1993; Zachos 2018a; Hoffman et al. 2024).

Microevolutionary evidence, including morphological, behavioral, and ecological variation, shows differentiation consistent with local adaptation or cultural divergence rather than speciation. Cranial distinctions are based on only two complete skulls and fall within the range of variation typical of populations within a single species (Rosel et al. 2021). Rice's whale possesses a distinctive acoustic repertoire and moderately deep-diving behavior (Soldevilla et al. 2017, 2022), but comparable ecological or vocal specializations occur among populations of other cetaceans (Coyne and Orr 2004). A 2003 stranding in North Carolina further suggests occasional extralimital occurrence, implying potential historical or sporadic contact with other Bryde's-like whales (Rosel et al. 2021).

Under an integrative framework, these findings indicate that Rice's whale exhibits microevolutionary divergence within an isolated population rather than clear macroevolutionary speciation. Following the unified species concept (de Queiroz 2007), diagnosability represents only one line of evidence for independent lineage evolution and must be corroborated by reproductive isolation, genealogical exclusivity, or ecological differentiation. At present, the weight of evidence rests primarily on mitochondrial data and subtle morphological traits derived from limited samples. Until comprehensive nuclear genomic analyses confirm sustained lineage independence, a conservative interpretation is warranted, recognizing Rice's whale as a regional subspecies or isolated variety within the Bryde's whale complex (Dayrat 2005; Padial et al. 2010; Zachos 2018b).

7 | Darwin's Caution and Taxonomic Judgment

Although Darwin recognized reproductive isolation as important, particularly noting that varieties typically produce fertile offspring whereas crosses between species often yield reduced fertility or sterility, he did not formally define species exclusively by reproductive isolation, a criterion later formalized by the Biological Species Concept (Darwin 1859; Mayr 1942). Darwin acknowledged that the criteria naturalists used to distinguish species (morphological gaps, distinctiveness, etc.) were pragmatic and that the true "mystery of mysteries" was how these gaps arise via natural selection. Modern evolutionary biology identifies multiple mechanisms by which new species can emerge (Avise 2000). Although allopatric speciation (geographic isolation) is often predominant, new species can also arise sympatrically (within the same geographic area through ecological or sexual divergence), parapatrically (in adjacent populations with limited gene flow), and, in rare instances, through hybrid speciation (formation of distinct lineages from interspecific hybrids) (Coyne and Orr 2004). Darwin focused on variation within and among populations and saw species boundaries as porous and subject to change. His caution about "vainly beating the air" over species versus variety is highly relevant in this discussion (Darwin 1859). He acknowledged that species delineation can be subjective and often relies on the collective judgment of experts.

In the case of Rice's whale, the decision to elevate it to species status was made by specialists after considering the available evidence, as proponents argued that the Gulf of Mexico whales represent a diagnosable lineage warranting recognition as a separate species (Rosel et al. 2021). However, Darwin cautioned against premature species naming based on scant evidence, and modern scholars echo this caution through the concept of taxonomic inflation, in which subspecies are elevated to species without compelling justification (Isaac et al. 2004; Burbrink et al. 2024). Thus, we must ask: Is Rice's whale a legitimate species or an example of taxonomic inflation? Darwin emphasized that common and widespread forms often yield wide varieties, thereby blurring boundaries between varieties and species (Darwin 1859). From this Darwinian perspective, the term *species* typically applies to the most common, widely distributed, or dominant forms, whereas *varieties* represent less divergent and more geographically restricted lineages within populations characterized by continuous variation and common descent without precise boundaries (Mayr 1969; Hennig 1966; de Queiroz 2007). Accordingly, Bryde's whale can be regarded as the widespread, dominant form, with Eden's whale and Rice's whale as derivative lineages. In this framework, Rice's whale is more appropriately considered a variety or subspecies of Bryde's whale rather than a distinct species.

Rice's whale is not numerically dominant today but represents an isolated lineage derived from a once widespread parent species, possibly shaped by a population bottleneck resulting from historical whaling or other demographic pressures. If, over evolutionary time, Rice's whale were to develop a significantly larger population size and geographic range, it might eventually be universally recognized as a distinct species. However, the infra- and interspecific character variation has not been thoroughly addressed, and the small population size makes its status as a species instead of a variety questionable. As Dayrat (2005) argued, no new species name should be created without careful treatment of infra- and interspecific character variation, and certainly not on the basis of only a handful of specimens.

Studying individual character variation is essential for species delineation, and diagnostic features should be present consistently across all specimens assigned to a species, but the limited number of Rice's whale specimens examined makes such analysis currently impossible. Obtaining multiple specimens of large whales is inherently challenging; however, this difficulty does not exempt researchers from adhering to rigorous scientific standards. Instead, it necessitates patience and determined, systematic data collection. Integrative taxonomy emphasizes that species hypotheses should be supported by multiple complementary lines of evidence, including morphological, molecular, reproductive, ecological, and behavioral data, rather than relying on single characters alone (Dayrat 2005; Padial et al. 2010). No new species should be designated based on fewer than a certain number of specimens, a threshold established by statistical significance and determined by specialists, especially in broadly distributed groups with numerous varieties, and certainly not from only a handful of specimens.

Modern systematics increasingly emphasizes integrative frameworks for species delimitation. de Queiroz (2007) argued that disputes over "species concepts" stem from treating properties of divergence, including reproductive isolation, diagnosability, monophyly, and ecological distinctness, as definitions rather than as evidence for independently evolving lineages. Genomic-scale data and multispecies coalescent models have advanced detection of cryptic divergence, although demographic processes can mimic speciation and risk taxonomic over-splitting (Fujita et al. 2012; Carstens et al. 2013; Sukumaran and Knowles 2017). Comparative studies in reptiles and amphibians show how these methods reshape taxonomy (Burbrink and Ruane 2021; Burbrink et al. 2024), while Hillis and colleagues stress combining genomic, ecological, and morphological evidence (Hillis 2019; Hillis et al. 2021). Zachos (2018b) cautions against recognizing every diagnosable isolate without macroevolutionary justification. Within this framework, Rice's whale exemplifies the challenges of balancing genomic diagnosability, ecological divergence, and limited morphological data against the risks of taxonomic inflation and the need to recognize genuine evolutionary diversity.

This modern perspective reframes the case for Rice's whale. The key question is not simply "is it a species?" but rather, "what evidence demonstrates that the Gulf of Mexico whales represent an independently evolving lineage?" Such evidence may come from mitochondrial monophyly, nuclear allele frequency divergence, osteological differences, ecological or behavioral distinctness, or reproductive isolation. None alone is definitive, but each adds weight to the case for or against lineage independence. Because neutral genetic differences can arise randomly through drift, species recognition based solely on such divergence must also demonstrate genealogical exclusivity, with independent, nonoverlapping lineages across multiple genes. Apparent drift-based divergence in small or bottlenecked populations may be transient and reversible through later gene flow, as illustrated by at least one instance in which Rice's whale occurred outside the Gulf of Mexico. Consequently, integrative taxonomy requires genetic, morphological, and ecological congruence before conferring full species rank (Dayrat 2005).

Recognition of Rice's whale as a distinct species ultimately depends on the degree to which genetic, morphological, and ecological data corroborate independent evolutionary history rather than recent demographic events. Darwin's caution remains instructive: premature designation based on single lines of evidence risks taxonomic inflation (Isaac et al. 2004; Zachos 2018b). Yet the unified and integrative frameworks emphasize that multiple, convergent properties, even if subtle, constitute positive evidence for lineage independence, while their absence weakens but does not disprove such independence.

Accordingly, Rice's whale should be evaluated within this evidentiary framework. Its mitochondrial diagnosability, subtle cranial morphology, restricted range, and distinct acoustic repertoire are each potential lines of evidence for lineage separation (Rosel and Wilcox 2014; Rosel et al. 2021; Soldevilla et al. 2022). However, the limited specimen base, reduced mtDNA diversity, and possible recent bottleneck effects (Hoelzel et al. 1993; Hoffman et al. 2024) warrant caution until additional nuclear genomic data provide a more robust test of independence. Lin et al. (2025) found that mitochondrial divergence between Eden's and Rice's whales (1.81%) is smaller than that between Eden's and Bryde's whales (2.94%) and falls within intraspecific ranges for other Mysticeti, emphasizing that mitochondrial diagnosability alone is insufficient to demonstrate species-level separation. Although the topology recovered by Lin et al. (2025) places Rice's whale as a distinct branch within the Bryde's whale complex, this preliminary phylogenetic signal must be interpreted cautiously, given the study's simplified demographic assumptions and limited genomic breadth. Moreover, their demographic models assume clean, sequential divergences without subsequent bottlenecks, an assumption inconsistent with the severely reduced and likely bottlenecked Gulf population.

Darwin's continuum perspective reminds us that all species originate from varieties, but de Queiroz (2007) emphasized that species are best understood as segments of separately evolving metapopulation lineages, with traits such as diagnosability, reproductive isolation, and ecological distinctness serving only as lines of evidence for lineage separation rather than defining criteria. Modern integrative taxonomy (Dayrat 2005; Padial et al. 2010) similarly stresses that the strength and concordance of multiple lines of evidence, rather than reliance on a single property, determine confidence in recognizing independent lineage evolution. Genetic diagnosability alone is not equivalent to speciation, but rather one potential line of evidence that must be evaluated in conjunction with convincing morphological, ecological, reproductive, and behavioral data, supported by a statistically significant sample size (Fujita et al. 2012; Carstens et al. 2013; Sukumaran and Knowles 2017; Hillis 2019).

8 | Conclusion and Recommendation

Moving forward, the species classification for Rice's whale will help focus conservation efforts specific to this Gulf of Mexico endemic while reminding us that the tree of life continues to branch in subtle ways. However, conservation actions can protect Rice's whale as a distinct population segment or subspecies without necessarily elevating it to species status, thereby avoiding potential taxonomic inflation (Isaac et al. 2004). Premature species designation without clear evidence of reproductive isolation or genealogical exclusivity undermines taxonomic rigor and diminishes the significance of genuine evolutionary divergence (Darwin 1859; Isaac et al. 2004). Consequently, researchers should strive to gather more comprehensive genetic data (e.g., whole-genome analyses from multiple individuals) and historical data to test the hypothesis of post-bottleneck genetic drift. Ultimately, a species designation should be supported by broad biological evidence (morphology, genealogical concordance, ecology, behavior, etc.) based on a sample size that can identify significant statistical differences. Darwin's perspective encourages us to treat species delineations as hypotheses about life's branching patterns, hypotheses that must be supported by evidence and remain subject to revision if new information arises.

In summary, Rice's whale exemplifies a case in which scientific analysis led to an executive decision to elevate a regional variety of Bryde's whale to species status, emphasizing the Phylogenetic Species Concept and genetic diagnosability (Taylor et al. 2017), despite lacking definitive evidence of reproductive isolation, genealogical exclusivity, or substantial adaptive divergence (Isaac et al. 2004; Bickford et al. 2007; Zachos 2018b). Consequently, tension exists between the genetics-focused approach to species delineation and the more integrative Darwinian perspective, prompting a critical question: At what point does genetic divergence within cryptic varieties, particularly when influenced by stabilizing selection and functional constraints and expressed as subtle morphological differences, justify their recognition as distinct species? Future genetic analyses of cetaceans may identify additional varieties appearing distinctive enough to qualify as species under specific phylogenetic criteria. However, their morphological and ecological differences may be subtle, having arisen primarily through genetic bottlenecks and drift resulting from commercial whaling and geographic isolation rather than through natural selection acting over long evolutionary timescales. Therefore, caution is essential to ensure that taxonomic distinctions reflect genuine evolutionary divergence rather than the unintended consequences of historical mass slaughter, geographic isolation, and genetic fragmentation.

Given this possibility, redefining the criteria for designating species and varieties of cetaceans may be necessary to avoid taxonomic inflation. A Darwinian approach would have favored treating Rice's whale as a subspecies, a local variety of Bryde's whale, until clearer evidence of irreversible divergence emerges. However, now that formal species designation has occurred, the priority moving forward should be the careful and rigorous evaluation of future cetacean taxonomic distinctions to guard against further species inflation. To do otherwise would be a regrettable lack of foresight for the future of cetacean taxonomy.

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R. W. Davis: conceptualization, writing – original draft, writing – review and editing.

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Conflicts of Interest

The author declares no conflicts of interest.

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