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Contribution of the Institute of Cetacean Research to the understanding of minke whale′s phylogeny and taxonomy

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ABSTRACT

In 1998 and based on early morphological and initial Japanese DNA studies in the 1990′s, two species of minke whales were re-specified, the Antarctic minke whale *Balaenoptera bonaerensis*, which is restricted to the Southern Hemisphere and the common minke whale *B. acutorostrata*, which is distributed globally. Furthermore, three sub-species of the common minke whale were recognized, one in the North Pacific, one in the North Atlantic and one in the Southern Hemisphere (dwarf minke whale). This paper summarizes the genetic and non-genetic studies conducted post 1998 by or in collaboration with the Institute of Cetacean Research, which were focused to confirm and/or refine the taxonomic classification proposed in 1998. As shown in this paper, results of those studies were consistent with the 1998 classification, which was the basis for the taxonomic status of minke whales currently agreed by the Committee of Taxonomy of the Society for Marine Mammalogy.

INTRODUCTION

Until the early 1980′s, only one species of minke whale was thought to exist, *Balaenoptera acutorostrata* Lacèpéde, 1804. This, despite early morphological studies that provided evidence of the existence of at least two species, one each in the Southern and Northern Hemisphere (e.g. Williamson, 1959; van Utrecht and van der Spoel, 1962; Kasuya and Ichihara, 1965; Omura, 1975).

From the start of the 1990′s comparative studies of minke whales were carried out based on genetic, morphology and ecological aspects, and on available samples from different oceanic basins (e.g. North Pacific, North Atlantic and Southern Hemisphere). This research effort was motivated in part by the reports in the mid 1980′s of a new ′form′ of minke whales in the Southern Hemisphere which was called as ′dwarf′ and ′diminutive′ minke whales that were different morphologically from the more abundant ′ordinary form′ minke whale distributed in the Southern Hemisphere (Best, 1985; Arnold, 1987).

Samples and data collected by the Institute of Cetacean Research (ICR) from different oceanic basins and southern ′forms′ of minke whale played an important role in the different analyses. Particularly, sixteen samples of the dwarf minke whale collected during early JARPA (Japanese Whale Research Program under Special Permit in the Antarctic) surveys contributed importantly in most of the genetic and non-genetic analyses of minke whale worldwide.

In the first half of the 1990′s results of some pioneering DNA studies confirmed the differentiation between the Southern and Northern Hemispheres minke whales suggested by historical morphological and morphometric studies. Furthermore, these genetic studies provided some highlights on the genetic diversity and differentiation of the southern ′dwarf form′. Wada *et al.* (1991) analyzed restriction fragment length polymorphism (RFLP) of mitochondrial DNA (mtDNA) in minke whales from the North Pacific and the Antarctic. The Antarctic sample included a single individual of the ′dwarf form′, which had been sampled during early JARPA surveys. North Pacific, southern ′ordinary form′ and southern ′dwarf forms′ were all genetically different. Furthermore, they found that the southern ′dwarf form′ and minke whales from the North Pacific were more similar to each other than they were to the southern ′ordinary form′. Pastene *et al.* (1994) expanded Wada *et al.* (1991) study to incorporate a larger number of the ′dwarf form′ sampled during JARPA (n=11). In addition to confirming the main results of Wada *et al.* (1991), for the first time they provided information on the level of mtDNA diversity of the southern 'dwarf form'.

Rice (1998) reviewed the early morphological studies cited above and the initial DNA studies in the 1990's described in the previous paragraph, and re-specified two species, the Antarctic minke whale *B. bonaerensis*, which is restricted to the Southern Hemisphere (called previously as southern 'ordinary form'), and the common minke whale *B. acutorostrata*, which is distributed globally. Furthermore, he recognized three sub-species of the common minke whale, one in the North Pacific, one in the North Atlantic and one in the Southern Hemisphere. The latter was called previously as southern 'dwarf form'. Rice's proposed minke whale species and sub-species are shown in Figure 1.

This paper summarizes the genetic and non-genetic studies conducted post-1998 by or in collaboration with the ICR, which were focused to confirm and/or refine the taxonomic classification proposed by Rice (1998).

GENETIC STUDIES

Genetic studies were expanded from the late 2000's by using different genetic markers and additional minke whale samples from different oceanic basins. Details of those studies can be found in Pastene *et al.* (2022) and a summary is presented below.

Figure 1. Species and sub-species of minke whales proposed by Rice (1998). From top to bottom: Antarctic minke whale, North Pacific common minke whale, North Atlantic common minke whale and Southern Hemisphere common minke whale (dwarf minke whale).

Phylogeny, speciation and radiation

The first study in the 2000's that involved samples of the minke whale worldwide was focused on understanding the radiation and speciation of minke whale in the context of climate changes (Pastene *et al.*, 2007). The study was based on mtDNA control region sequences (340 bp) in samples from the Antarctic minke whales (previously labeled as 'ordinary form') (n=180), North Atlantic (n=102), North Pacific (n=161) and Southern Hemisphere (previously labeled as 'dwarf form') (n=23) common minke whales. A total of 187 haplotypes (unique sequences) were determined in the total sample, several phylogenetic and population genetic analyses were conducted. The study provided evidence for phylogenetic differentiation not only between the two species of minke whales but also among North Atlantic, North Pacific and Southern Hemisphere common minke whales. The study estimated that the two species of minke whales diverged in the Southern Hemisphere less than 5 Ma, and that the current sub-species of the common minke whales diverged after the Pliocene some 1.5 Ma. Furthermore, based on their analyses in the minke whales, the authors proposed the hypothesis that prolonged periods of global warming facilitate speciation in pelagic marine species that depend on upwelling.

The next study (Pastene *et al.*, 2010) used mtDNA control region sequences (327 bp) and a similar sample set as that used in Pastene *et al.* (2007) but this time the study was focused to elucidate the population genetic structure of the Southern Hemisphere common minke whales (dwarf minke whales) using samples from western South Atlantic (WSA, n=12-Brazilian-Chilean samples) and western South Pacific (WSP, n=17-JARPA samples) (Figure 2).

Phylogenetic inferences derived from different methods were consistent, and similar to the inferences obtained in the previous study by Pastene *et al.* (2007). WSA common minke whale haplotypes (except one), clustered in a single clade, which nested within the North Atlantic common minke whale clade. On the other hand, WSP common minke whale haplotypes were clustered in a different clade. The study showed that haplotypes from the WSA whales share a more recent common ancestors with the North Atlantic minke whales than they do with the WSP minke whales. The analysis suggested a very low number of migrants by generation between WSA and WSP, which suggest that the WSA single haplotype in the

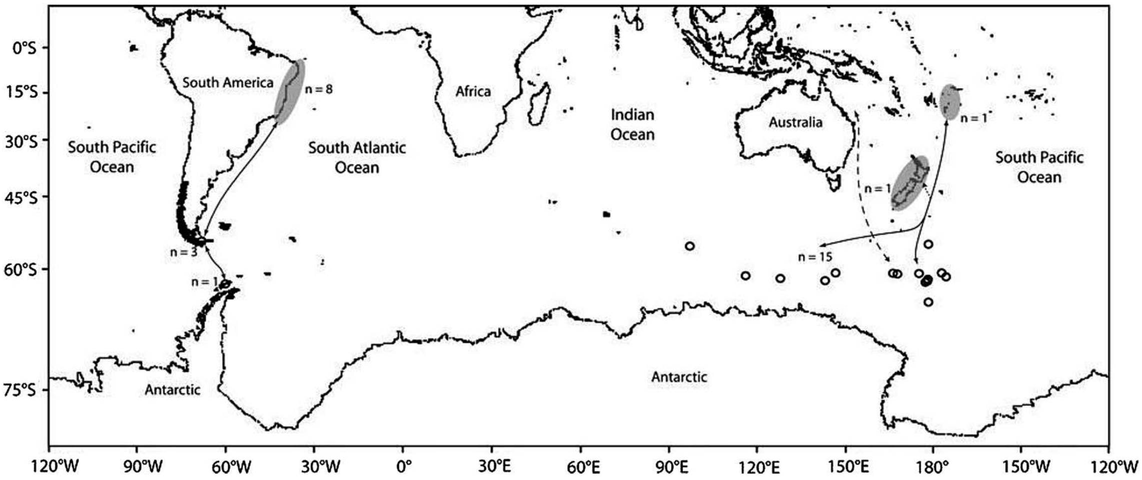

Figure 2. Geographic position of Southern Hemisphere common minke whale (dwarf minke whale) samples used in Pastene *et al.* (2010). Solid and dashed lines indicate possible migratory routes and possible connections, respectively (modified from Pastene *et al.*, 2010).

WSP clade was unlikely to be a result of migration but rather due to incomplete lineage sorting.

A more recent genetic analysis on minke whales worldwide conducted in cooperation with ICR was based on mtDNA control region sequences (313 bp) and microsatellite DNA (msDNA) (11 loci) (Milmann *et al.*, 2021). The sample set for the mtDNA analysis was similar to those in previous studies but the samples of the Southern Hemisphere common minke whales were increased (WSP, n=17; WSA, n=30), and msDNA was used in addition to mtDNA. A total of 148 haplotypes were determined in the total sample. The genealogy of the mtDNA haplotypes was estimated using several methods. These methods provided similar results, and they were consistent with previous phylogenetic inferences. Results from the Bayesian inference method are shown in Figure 3. This figure shows two main clades, one corresponding to Antarctic minke whale and the other to common minke whales. Furthermore, within the common minke whale clade, North Pacific, North Atlantic and Southern Hemisphere common minke whales clustered in different sub-clades.

Figure 3 shows that WSA and WSP common minke whales in the Southern Hemisphere clustered in different sub-clades (except the single WSA haplotype mentioned previously that clustered within the WSP sub-clade), and that the WSA haplotypes fell with the North Atlantic sub-clade. This study also estimated the net nucleotide substitutions (d_A) (Nei, 1987) between species and subspecies of minke whales. The d_A between Antarctic and common minke whales was high (0.08 in average). The value among common minke whales from different oceanic basins averaged 0.026. The d_A between Southern Hemisphere WSP and WSA was 0.027 and that between Sea of Japan and western North Pacific was 0.007.

The msDNA analysis in Milmann *et al.* (2021) involved samples from three localities only: North Pacific and Southern Hemisphere (WSA and WSP) common minke whales. Unfortunately, no samples from the North Atlantic common minke whales were available for this analysis. The pattern of msDNA differentiation was investigated by two indexes F_{ST} and D_{SW}. All pairwise comparisons among North Pacific, WSA and WSP yielded statistically significant differences, and the values estimated between WSA and WSP were smaller than the values between each of these populations and North Pacific common minke whales. Therefore, North Pacific, Southern Hemisphere WSA and WSP not only were separated phylogenetically in their mtDNA but they differed significantly in their msDNA as well.

In a cooperative study with ICR, Glover *et al.* (2013) provided information on genetic differentiation between Antarctic and common minke whales species as well as among common minke whales from different oceanic basins. The study was based on mtDNA control region sequences (287 bp) and msDNA (11 loci), and samples from the Antarctic minke whale (n=91), North Atlantic (n=91), North Pacific (n=95) and Southern Hemisphere (WSP) (n=9) common minke whales. The genealogy of the mtDNA haplotype was similar to the previous studies. The msDNA F_{ST} estimates were calculated, and Bayesian cluster analysis was also performed using the program *STRUCTURE* (Pritchard *et al.*, 2000). Pairwise F_{ST} estimates revealed that the Antarctic minke whales, North Atlantic, North Pacific and Southern Hemisphere (WSP) common minke whales were genetically distinct from each other.

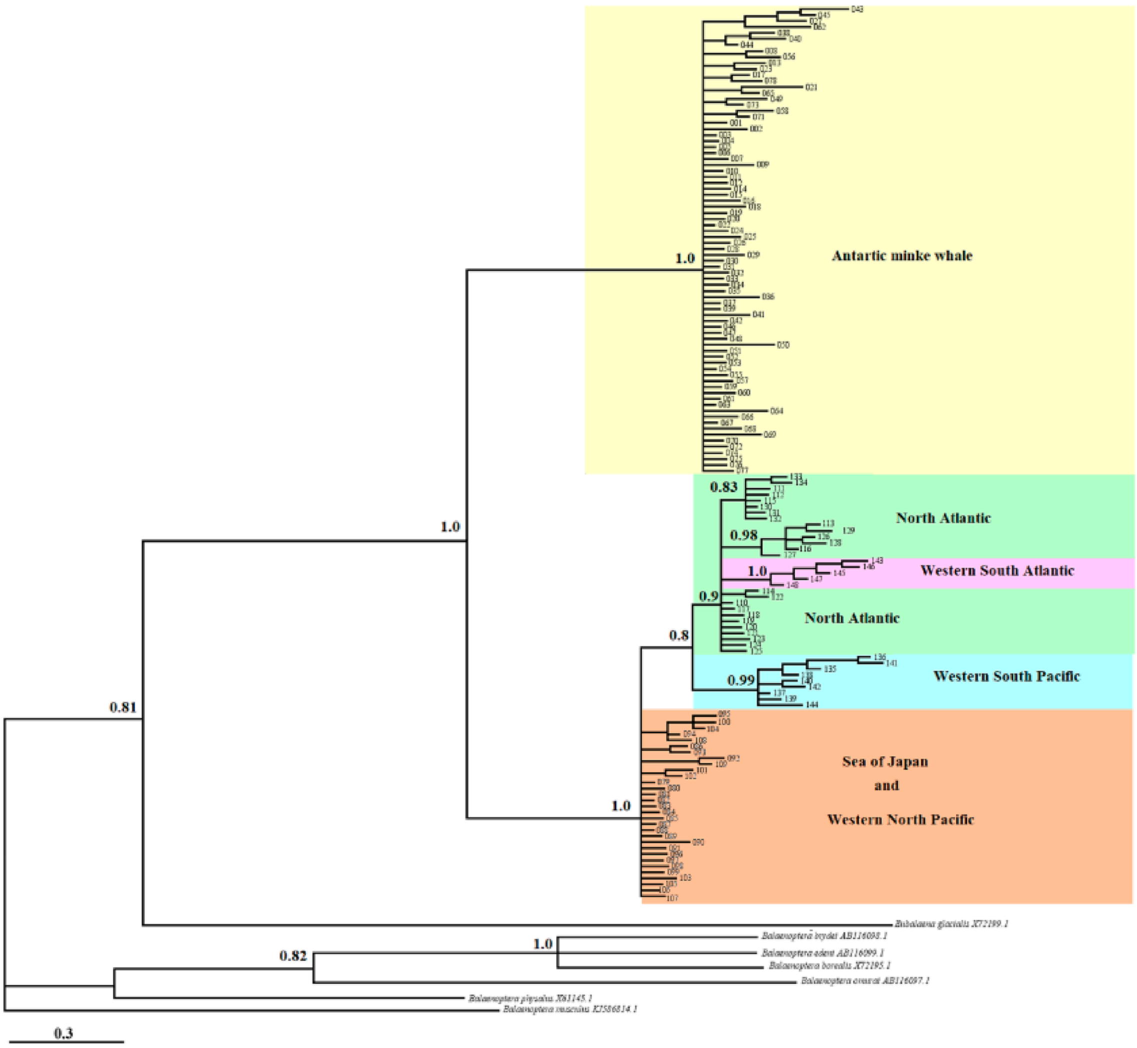

Figure 3. Bayesian phylogenetic tree of minke whale mtDNA haplotypes. Values indicate support for each node according to the maximum posterior probabilities>80%. Scale bar represents substitutions per nucleotide site (modified from Milmann *et al.*, 2021).

Also, the Bayesian cluster analysis supported the results based upon F_{ST} exhibiting large genetic differences between Antarctic and common minke whales as well as among common minke whales from North Atlantic, North Pacific and Southern Hemisphere (WSP).

Minke whale hybridization and unusual migration event

A genetic study based on both mtDNA (287 bp) control region sequences and msDNA (13 loci) conducted in cooperation with ICR, reported the migration of an Antarctic minke whale into the Arctic Northeast Atlantic in 1996 (Glover *et al.*, 2010). The same study reported the occurrence of a hybrid whale in the North Atlantic in 2007. The latter used a genetic baseline consisting of the three minke whale species and sub-species which had large sample size (Southern Hemisphere common minke whales were excluded due to their small sample size). The 2007 hybrid was demonstrated to consist of maternal contribution from Antarctic minke whale and most likely paternal contribution from North Atlantic common minke whale. Another case of hybrid was identified using the same analytical procedures. It was a pregnant female captured in 2010 (Glover *et al.*, 2013). In this case, the genetic analyses by both markers confirmed that the mother was a hybrid displaying maternal and paternal contribution from North Atlantic common and Antarctic minke whales, respectively. This study demonstrated for the first time that hybrids between minke whale species may be fertile, and that they can backcross.

It is very possible that the migrations from Antarctic to North Atlantic informed above were random events, which may or may not represent a scouting behavior having occurred over many years. The Northeast Atlantic does not appear to be a major destination of Antarctic minke whale migration outside its previously documented distribution (Glover *et al.*, 2010). However, it is possible that unusual migration patterns e.g. Southern-Northern Hemispheres migrations, could increase in the future as an effect of climate changes, particularly global warming which is making possible new migration routes.

NON-GENETIC STUDIES

The most comprehensive study focused on investigating differences in morphology, growth and life history of Southern Hemisphere common minke whales (dwarf minke whales) in relation to minke whales from different oceanic basins was carried out by Kato *et al.* (2021). This study was based on the examination of 16 dwarf minke whales, three males and 13 females, sampled by JARPA in the Indo-Pacific sector of the Antarctic (called as WSP in the genetic analyses) between 1987/88 and 1992/93 austral summer seasons. Kato *et al.* (2021) examined several aspects of their biology and life history, some of which were compared with those in Antarctic minke whales, North Pacific and North Atlantic common minke whales. Relevant results of their analyses are summarized below.

Body size and growth: female dwarf minke whales were significantly smaller in body length than Antarctic and North Pacific common minke whales through all age-classes. The mean asymptotic lengths indicated that fully grown females dwarf minke whales (physical maturity) was reached at 7.16 m, about 2.0 m and 1.5 m shorter than Antarctic minke North Pacific common minke whales, respectively.

Body length-weight relationship: this analysis suggested that dwarf minke whales tended to be stockier than Antarctic minke whales.

External appearance: the pattern of dark throat extension, shoulder flipper pigmentation and thorax blaze/patches pattern distinguished clearly dwarf minke whales from Antarctic and North Pacific minke whales. In particular, the dwarf minke whale possesses a distinct white flipper mark that is characteristic of the species in the Northern Hemisphere and absent in the Antarctic minke whale. The difference with the Northern Hemisphere whales is that the white flipper extends onto the shoulder in the dwarf minke whale (see Figure 1).

Baleen plate coloration: the external view of a baleen plate series of dwarf minke whales is mostly bilaterally symmetrical in coloration with a creamy white anterior portion that extends for almost half of the entire length of the baleen plates. The Antarctic minke whale in contrast has a bilaterally asymmetric baleen plate coloration. On the other hand, North Pacific common minke whale has usually all creamy white baleen plates.

Skeletal features: there were longer rostrum, deeply curved mandible and narrower nasal bone in dwarf minke whales in comparison with Antarctic and Northern Hemisphere common minke whales.

Morphometry: ANCOV analyses revealed significant differences in both external body and skull morphology among dwarf, Antarctic and Northern Hemisphere common minke whales. A cluster analyses of the skull morphology showed differentiation between dwarf minke whale and Antarctic and Northern Hemisphere common minke whales. Interesting, dwarf minke whales were more closely related to North Atlantic common minke whales, which coincide with the results of some of the genetic analyses shown above.

Life history: length at sexual maturity in female dwarf minke whales was estimated around 6.0–6.5 m, which was 1.0–2.0 m smaller than Antarctic and Northern Hemisphere common minke whales. The maximum life span in female dwarf minke whales was estimated at 47 years, which was similar to Antarctic minke whale (50 years) and North Pacific common minke whale (48 years).

Nakamura *et al.* (2018) examined morphological differences of the white patch on the flipper between North Pacific and North Atlantic common minke whales. There were statistical significant differences between common minke whales from the two oceanic basins in two measurements: the length between the tip of flipper to the proximal border of white patch relative to the total flipper length, which was larger in the North Atlantic (74.3%) than in North Pacific (63.6%), and in the mean angle between the proximal boundary line of the white patch and the longitudinal axis of the flipper, 70.1% and 92.3% in North Atlantic and North Pacific common minke whales, respectively.

From the practical point of view, the two species in the Southern Hemisphere have not been confused during the sighting surveys conducted using closing mode because of the distinctive morphological features of the two species. According to the descriptions for identification on the two species by Kato *et al.* (2015), the two species can be clearly distinguished from the vessels by the presence of white patch overspread on the shoulder-flipper portion in dwarf minke whales in contrast to Antarctic minke whales which lack them. The Antarctic minke whale can be distinguished in the field by its larger size and by a dorsal fin that is set farther back on the body. The dwarf minke whale has a very distinctive white patch on its flipper, unlike the light gray flipper of the Antarctic minke whale.

CURRENT TAXONOMIC STATUS OF MINKE WHALES

All post-1998 studies described above are consistent with the classification proposed by Rice (1998) and therefore these studies have contributed to the current taxonomic classification of minke whale by the Committee of Taxonomy of the Society for Marine Mammalogy, which is based largely on the classification by Rice (1998). The Committee listed the following species and sub-species of minke whale (Committee of Taxonomy, 2025):

(1) *Balaenoptera acutorostrata* Lacèpéde, 1804. Common minke whale
  (a) *B. a. acutorostrata* Lacèpéde, 1804. North Atlantic minke whale
  (b) *B. a. scammoni* Deméré, 1986. North Pacific minke whale
(2) *Balaenoptera bonaerensis* Burmeister, 1867. Antarctic minke whale.

The Committee also presents a 'List of proposed unnamed Taxa', which includes:

Balaenoptera acutorostrata un-named subsp. Dwarf minke whales (Rice, 1998).

It should be noted that the analyses summarized above suggested that common minke whales from the WSP and WSA in the Southern Hemisphere are phylogenetically separated, which could have taxonomic implications that should be further examined in the future. As demonstrated above, the genetic and non-genetic analyses conducted by or in collaboration with the ICR contributed largely to advance in the clarification of the taxonomic status of minke whales agreed currently by the international scientific community and in addition, evidenced new scientific challenges that should be addressed in future.

ONGOING AND FUTURE STUDIES

Further genetic analyses of minke whales from different oceanic basins should be conducted based on mitochondrial sequences and nuclear markers (microsatellite DNA), with emphasis on the southern common minke whales. While samples of this sub-species from the WSP (mainly JARPA samples) and WSA (Brazilian and Chilean samples) have been analyzed suggesting phylogenetic differentiation between the two oceanic basins, further analyses from other localities, e.g. South Africa should be conducted. On this regard, some few samples from the South African common minke whale are being analyzed currently. These genetic analyses should be complemented with additional morphological and morphometric analyses based on available data from the North Atlantic and Brazilian common minke whales. New genetic approaches such as Whole Genome Sequencing (WGS) should be used to investigate minke whale differentiation and genes responsible for local adaptation.

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