



Original investigation

## Phylogeography of the finless porpoise and potential implications for the taxonomy of *Neophocaena* spp.

Wenzhi Lin<sup>a,b</sup>, Leszek Karczmarski<sup>b,c,\*</sup>, Yuping Wu<sup>a,\*</sup>

<sup>a</sup> South China Sea Bio-Resource Exploitation and Utilization Collaborative Innovation Center, Guangdong Provincial Key Laboratory of Marine Resources and Coastal Engineering, Zhuhai Key Laboratory of Marine Bioresource and Environment, School of Marine Sciences, Sun Yat-Sen University, Guangzhou, 510275, PR China

<sup>b</sup> The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Hong Kong

<sup>c</sup> Cetacean Ecology Lab, Cetacea Research Institute, Hong Kong

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## ABSTRACT

The finless porpoise (genus *Neophocaena*) is a poorly known cetacean of great conservation concern. Within its range, from western Pacific to northwestern Indian Ocean, there are currently two species recognized (*N. asiaeorientalis* and *N. phocaenoides*), thought to be reproductively isolated since last glacial maximum, with the only sympatric overlap zone in Taiwan Strait. However, the genetic variation across the genus' distribution has not yet been extensively studied, especially in the Indian Ocean. We performed an exhaustive review of molecular data of the finless porpoise across its range. Neighbor-net networks analyses based on two mitochondrial loci (control region/CR and cytochrome *b*/cyt *b*) suggest that finless porpoises from the Indian and Pacific Ocean constitute two distinct clades, well-defined by fixed mutations at both loci. A molecular clock analyses indicate early split (CR: 13.1 Ma, cyt *b*: 12.9 Ma) between these two oceanic lineages, while spatial genetic analyses further suggest that in the Pacific the divergence was primarily due to the taxon from Japanese waters rather than inter-species divergence across the Taiwan Strait. As extinction risks can be substantially underestimated if threatened species are pooled together with non-threatened, especially in the absence of long-distance migration, we suggest that the present 2-species taxonomy of the genus *Neophocaena* should be given further examination, with concerted sampling effort in the Western Indian Ocean. More research effort and genomic information is needed before taxonomic revisions can be considered; such further studies are strongly recommended as they may affect the current status classification of the species constituting the genus *Neophocaena*. Most notably, the narrow-ridged finless porpoise off Japan merits urgent conservation attention.

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## Introduction

The finless porpoise (genus *Neophocaena*) is a small coastal toothed cetacean under the family Phocoenidae. Its range extends from waters off central Japan and the Korean Peninsula, south along the coast of China to Southeast Asian waters, and further westwards along the northern rim of the Indian Ocean to the Persian Gulf (Amano, 2009). As the finless porpoise occurs mostly in shallow coastal waters, with much of its range heavily exploited by coastal fisheries, these animals are frequently a victim to bycatch, especially by gillnets (Jefferson and Curry, 1994; Shirakihara and Shirakihara, 2013) and their populations are thought to be decreasing

in abundance throughout the genus range (Wang and Reeves, 2012b, 2012a). Population estimates have so far been generated only in a few locations at the northern edge of genus distribution, and all of them indicate a dramatic decline over the past decades; e.g. the Yangtze River (Mei et al., 2014), Ariake Sound, Tchibana Bay and Inland Sea, Japan (Hashimoto et al., 2015; Kasuya et al., 2002; Shirakihara and Shirakihara, 2013) and waters off the Korean Peninsula (Park et al., 2015). Meanwhile, very little is known of the finless porpoise throughout the rest of its range, and the conservation efforts are meagre.

The latest taxonomic revision of the genus *Neophocaena* proposed two species, the narrow-ridged finless porpoise *Neophocaena asiaeorientalis* in waters north of Taiwan Strait, which was further divided into two sub-species, the marine *N. a. sunameri* (Pilleri and Ghir, 1975) and freshwater *N. a. asiaeorientalis* (Pilleri and Ghir, 1972) in the Yangtze River; and the Indo-Pacific finless porpoise *N. phocaenoides* (Cuvier, 1829G. Cuvier, 1829), exclusively marine,

\* Corresponding authors.

E-mail addresses: [leszek@hku.hk](mailto:leszek@hku.hk) (L. Karczmarski), [exwyp@mail.sysu.edu.cn](mailto:exwyp@mail.sysu.edu.cn) (Y. Wu).

found in tropical and subtropical waters from Taiwan Strait in the east to the Persian Gulf in the west (Jefferson and Wang, 2011). The Taiwan Strait is the only known sympatric zone where both species co-occur. So far, the taxonomy of the genus relies primarily on morphological characteristics, of which only the tubercle patch and dorsal ridge separates the two currently recognized species (Jefferson and Wang, 2011). Other features, such as the cranial morphology, which is more widely used in taxonomic studies of marine mammals, provided ambiguous classification of the taxon; e.g. Amano et al. (1992) noted that finless porpoise from the Indian Ocean had shorter and wider rostrums compared to those from the Pacific region. This difference, however, was less evident when larger sample sizes from more sampling locations were examined (Jefferson, 2002).

In conservation practice, the concept of a species has far going implications. For range-restricted taxa, poor understanding of taxonomy may lead to wrong interpretation of the range and ranging pattern of a species, which could further result in an underestimation of extinction risks (Fennessy et al., 2016). Thus, correct taxonomic classification is instrumental in the formulation of informed conservation and management strategies. In the past decades, there has been an increasing use of phylogenetic species concept (PSC), accompanied and facilitated by recent advances of genetic techniques and analytical tools (Mallet, 1995). The PSC does not just describe the distribution pattern of genetic diversity, but, together with other relevant information such as paleogeographic history, it helps in understanding how the current pattern first appeared and how it was maintained. In other words, it facilitates a better understanding of the evolutionary processes of the formation of taxon (Cooke et al., 2012; Luhariya et al., 2014).

In the case of the finless porpoise, however, genetic studies had only access to opportunistically obtained samples from stranded or by-caught animals, limited in quantity and collected exclusively in warm waters of northwestern Pacific and the Yangtze River system. Consequently, these regional datasets have to be viewed cautiously, which has sometime been overlooked. For example, Wang et al. (2008) proposed that in Taiwan Strait, the *N. sunameri* and *N. phocaenoides* were reproductively isolated since the last glacial maximum. This study was subsequently used as a prime genetic evidence for the current two species taxonomy (Jefferson and Wang, 2011). However, Wang et al. (2008) focused exclusively on the sympatric zone in the Taiwan Strait, while the divergence outside this area was poorly quantified.

In tropical waters, the taxonomy of the Indo-Pacific finless porpoise is even less certain. The lack of genetic structure in the South China Sea (Chen et al., 2010) has been challenged by a recent study with a larger sample size, which revealed that the genetic divergence within the northern South China Sea is comparable to that of the inter-species level across the Taiwan Strait (Jia et al., 2014). A follow-up study by Lin et al. (2014) suggested that both the ranging behavior of the porpoises and climatic events on a larger geographic scale are responsible for the pattern of the genetic structure of this genus. With more genetic data obtained recently from the finless porpoise in the Indian Ocean (Jayasankar et al., 2008), there is now an opportunity to test the recently proposed stepwise-divergence-hypothesis (Lin et al., 2014), which so far has not yet been fully utilized.

The aim of the present study is to assess the phylogenetic relationship between the finless porpoise from the Indian Ocean, the western Pacific Ocean, and from the Yangtze River using two mitochondrial loci (control region/CR and cytochrome *b*/cyt *b*), which are both widely used for the divergence study at a species level (Randi et al., 2001). This study contributes to the evaluation and testing of our recently proposed multi-step divergence hypothe-

sis (Lin et al., 2014), and for the first time sheds more light on the taxonomic status of the finless porpoise in the Indian Ocean.

## Material and methods

### Sample collection

Sequences of both the control region (CR) and cytochrome *b* (cyt *b*) were collected from the GenBank, which covered a wide range of the genus distribution (Fig. 1). For the CR, sequences were collected for *N. a. asiaeorientalis* from the Yangtze River (51); *N. a. sunameri* from the East China Sea (16), the Yellow Sea (18), the Bohai Sea (142), the Omura Bay (8), the Ariake Sound and Tachibana Bay (65), the Inland Sea (30), the Ise-Mikawa Bays (56), and the Sendai and Tokyo Bay (14); and *N. phocaenoides* from the Taiwan Strait (33), the Pearl River Delta (78), the west coast of India (12) and the Persian Gulf (1, sampling information is available on <http://plan4theland.org/>, accessed on 18 Sept 2016). For cyt *b*, sequences of 123 individuals of *N. a. sunameri* were obtained, 111 from the Bohai Sea and 12 from waters off the Korean Peninsula; and 90 individuals of *N. phocaenoides* sampled in the Pearl River Delta (78) and off the west coast of India (12). However, it should be noted that many published sequences were not identified by morphological characteristics, but rather based solely on sampling location (Li et al., 2011; Yang et al., 2002). Given that the Taiwan Strait is the only recognized sympatric zone for the two species, the misidentification of taxon may be less likely in the Yellow/Bohai Sea (Li et al., 2011), but the 33 sequences reported by (Yang et al., 2002) should be treated with caution. To further exclude the possible bias caused by unreliable data, information of every sequence, including the sampling location, stranding date and the species identity were carefully examined and compared with the information in the source references. Seventeen sequences of CR (HM106471–HM106486, HM063471) and 19 of cyt *b* (HM137083–HM137101) that did not have information on the relevant source reference and sampling location were excluded from further analyses. The final dataset consisted of 524 and 213 sequences (individuals) of CR and cyt *b*, respectively (Table 1).

### DNA-based analysis

To define the grouping pattern of populations, we used a spatial analysis of molecular variance (SAMOVA 2.0) which optimized the grouping with the lowest geographic proximity and maximum genetic differentiation (Dupanloup et al., 2002). These analyses were run for CR data only because it was the most commonly used marker and covered a broader range compared to the available cyt *b* sequences (Fig. 1), which included five populations from waters off Japan (*N. a. asiaeorientalis*), and one population each from Yellow/Bohai Sea (*N. a. asiaeorientalis*), East China Sea (*N. a. asiaeorientalis*), Yangtze River (*N. a. sunameri*), Taiwan Strait (*N. phocaenoides*) and the Pearl River Delta (*N. phocaenoides*). Thirty individuals were randomly selected from each of these sampling sites whenever possible. Twelve samples of *N. phocaenoides* from the west coast of India, including Gangoli, Malpe and Mangalore, were combined into one population due to close proximity and shared haplotypes. One sequence from the Persian Gulf (*N. phocaenoides*) was also included and treated as one population. The optimal grouping pattern of sampled sites was automatically searched without prior assumptions with *K* ranging from 2 to 12. For each run of SAMOVA, 100 independent annealing processes were simulated to overcome the possible bias associated with the starting *K* value. As SAMOVA considers only the linear distance between sampling sites, the divergence caused by a geographic barrier may be underestimated. Thus the genetic structure of finless

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