Revision of the taxonomy of finless porpoises (genus Neophocaena): The existence of two species

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Abstract

Due to extensive morphological variation and inadequately-sampled or poorly-designed studies, the taxonomy of the finless porpoises (genus *Neophocaena*) has been controversial for some time. An uneasy stability with the arrangement of finless porpoises into a single species consisting of three subspecies dominated for many years. However, in the past decade new data examining both morphological and molecular characters provided strong evidence for the existence of at least two distinct biological species, by demonstrating a lack of interbreeding in sympatry between the two major morphological forms of finless porpoises. All finless porpoise specimens examined have had either a wide dorsal tubercled area or a much-narrower one, and there appears to be no overlap between the two species in this feature. Furthermore, the two species have apparently been reproductively isolated since the last glacial maximum, about 18,000 years ago. Taxonomic studies of finless porpoises are reviewed, the widely-accepted view of one species is rejected, and the two recognized species are redescribed. The revised taxonomy of the finless porpoises includes the Indo-Pacific finless porpoise (*Neophocaena phocaenoides*) and the narrow-ridged finless porpoise (*N. asiaeorientalis*), with two subspecies (Yangtze finless porpoise, *N. a. asiaeorientalis,* and East Asian finless porpoise, *N. a. sunameri*) within the latter species. [JMATE. 2011;4(1):3-16]

Introduction

Finless porpoises have a large geographic range; they are distributed in a ribbon-like manner in shallow, coastal waters around the Indian and western Pacific oceans from the Persian Gulf to most of the Indo-Malay region and then northward through the waters of China (including the lower to middle reaches of the Yangtze River) to southern Japan and Korea (15, 16). Several morphological forms of finless porpoises have been described, with the first reliable reports of geographical variants by Fraser (6), who observed apparent differences in a small sample of Japanese and Chinese finless porpoise skulls, and suggested that there may be multiple species of finless porpoises. Finless porpoise taxonomy and systematics have been somewhat controversial for many decades (14, 15, 16). In the 1800s, four species of finless porpoise were described, most based on single specimens (3, 29, 21, 20), but due to the lack of any rigorous systematic studies examining the variation within the genus sufficiently, a conservative arrangement with only one species (*Neophocaena phocaenoides*) was recognized through the latter half of the twentieth century (27). In this paper, we review information from multiple lines of evidence for the existence of two species of finless porpoises, redescribe both species (complete with illustrations) and examine their distributions.

Morphology of the Dorsal Structures

There has been much confusion amongst researchers in the description of the dorsal morphology of finless porpoises. All finless porpoises have a unique structure on the back that replaces the dorsal fin found on most other cetaceans (Figure 1). This structure has variously been called the dorsal ridge, dorsal groove, or tubercle(d) area (or other variations thereof), and although the morphology is quite different in the two species described here (see below), the dorsal structures are clearly homologous, as there is nothing closely related in morphology in other extant delphinoid cetaceans, including other phocoenids. Unless clarity is brought to the terminology used to describe these structures, confusion will continue.

There are three main important features that can be used to describe the dorsal surface of any finless porpoise and we define them here to prevent further misunderstanding of the structures being described:

Dorsal ridge – refers to a clearly raised (can be up to 5 cm high and almost fin-like, long, thin projection running along the mid-line of the back that is found

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anterior of, but merging smoothly with, the caudal peduncle region (usually arising from somewhere between the flippers and the mid-point of the body). Along the entire (more or less) dorsal surface of the ridge are numerous bumps or prickles called tubercles (Figure 1). There is great individual variability with the ease of determining the origin of the ridge and the seamless transition into the caudal peduncle makes differentiating the end of the ridge from the start of the caudal peduncle quite difficult. As a consequence of the subjectivity in identifying the anterior and posterior ends of this structure, ridge length measurements in the literature are of limited value for comparison across individuals and studies. For some individuals (of *N. phocaenoides*), the width of the ridge can not feasibly be measured, because difficulties may exist in identifying the presence of a clear ridge. Even on *N. asiaeorientalis*, where the dorsal ridge is obvious, the width of the ridge may not be straightforward. On some individuals, the dorsal ridge tapers smoothly from the base to the dorsal surface (the ridge appearing triangular in cross-section).
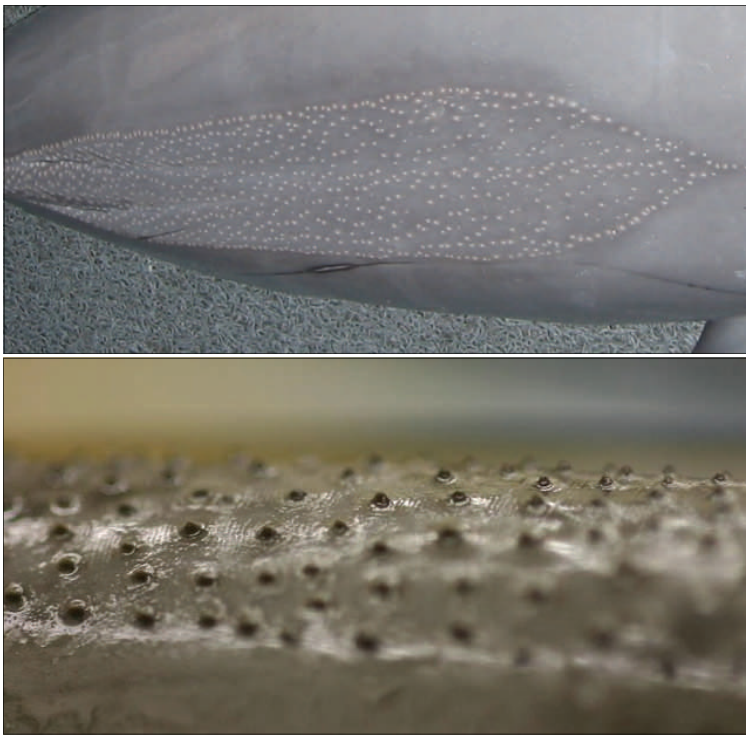

Figure 1 - Close-up views of the structure of the dorsal patch and tubercles: *N. phocaenoides* (a) and *N. asiaeorientalis* (b). Photos by TAJ and JYW.

Dorsal grooves – in general, two kinds of dorsal grooves have been observed on finless porpoises. The central groove is a concavity that can be present on both species and is found usually from the flippers to about mid-length of the animal. The depth of this groove varies individually and across species, and it can also be absent on some individuals or populations. When a dorsal ridge is clearly present, the central groove is bifurcated into two lateral grooves that run along each side of the ridge. However, determining where the central groove becomes lateral grooves can be problematic if the origin of the ridge is not clearly de-marcated and rises slowly as the transition between cen-tral and lateral grooves will also occur gradually along a considerable portion of the back. At least for many individuals of *N. asiaeorientalis* from Japanese waters, dorsal or lateral grooves do not appear to be present. For *N. phocaenoides*, the lateral grooves may be absent or, if present, are poorly-developed and the central groove may also be absent, being replaced instead by a flattened area upon which the tubercled patch sits. Because of previous terminology issues, the great individual variation that exists and difficulties in measuring these structures, efforts to quantify these structures have been more or less absent and may be of little value. The most important piece of information may be simply presence/absence of these structures.

Tubercled patch – found on the skin along the center of the dorsal surface, and for individuals with ridges, the tubercles run along the top of the ridges and onto the tail stock. This patch is comprised of numerous, small and well-innervated tubercles (17, 18) that are arranged loosely into longitudinal rows but in various patterns. The appearance of the tubercles can vary greatly as well, from being pointed prickles (sometimes with what appears to be a spine) to blunt bumps. Describing the tubercled patch has mainly involved measuring its greatest width, length and counting the number of rows of tubercles across the widest part of the patch. There is usually little difficulty in measuring the greatest width of this structure but measuring the length of the patch and sometimes counting the number of longitudinal rows has not always been straightforward. With measuring length, locating the most anterior and most posterior tubercles is often difficult, even on fresh

specimens and can be nearly impossible on dessicated or decomposed specimens. Observer variability in counting the number of tubercles is also likely to occur, due to the loose arrangement of the tubercles on some specimens. However, even with such observer variability, the obvious differences across the two main forms have not been obscured. Standardizing the collection of this information may be useful for furthering our understanding of finless porpoise taxonomy.

Review of Previous Studies

In the 1970s, Giorgio Pilleri and his colleagues (23, 24, 25, 26), conducted extensive (albeit largely qualitative) taxonomic studies on the genus. They documented a great deal of geographic variation in coloration, external morphology and skeletal morphology exhibited by finless porpoises and suggested that three species be recognized: *Neophocaena phocaenoides* in the Indian Ocean, *N. asiaeorientalis* in the Yangtze River of China, and *N. sunameri* in Korea and Japan. Their studies were flawed by a lack of recognition of the limitations of observed differences based on very small sample sizes. Although most subsequent authors accepted the geographic variation as real, the differences between the forms were generally not thought to warrant species-level distinction (e.g., van Bree (31) considered the differences between Chinese and Japanese finless porpoises to be taxonomically insignificant). Gao (7) and Gao and Zhou (8, 9, 10) conducted detailed, quantitative taxonomic investigations using multiples lines of evidence and large samples (although all of their specimens were from Chinese waters) and also concluded that *Neophocaena* was monotypic, but contained three well-differentiated subspecies: *N. p. phocaenoides* in the Indian Ocean to the waters of southern China, *N. p. asiaeorientalis* in the Yangtze River (China), and *N. p. sunameri* in the marine waters of the northern half of China, Korea and Japan. Additional systematic studies, conducted by P. Wang (37, 38) and Amano et al. (1), also reached similar conclusions. However, a common problem with all of these studies was a weak study design that was often compounded by limited sampling (e.g., using geographic location as the basis of *a priori* classifications for analyses of specimens obtained from areas of known,

suspected or likely sympatry of more than one form of porpoise).

In the past two decades, a number of molecular genetic studies were conducted on the finless porpoises (2, 11, 39, 40, 41, 42, 43, 44, 45, 46, 47, 54). In general, the results of these studies supported the existence of the three forms recognized by Pilleri and his colleagues, but all authors considered the differences observed only warranted subspecies level distinction, as was suggested earlier (7, 8, 9, 10, 37, 38). However, none of the molecular or previous morphological studies were designed to address species-level alpha-taxonomy (or were poorly designed to do so), due to a lack of any theoretical basis for testing the existence of multiple species (i.e., they also suffered from the same study design problems as with the morphological studies described above). As such, the erroneous conclusions regarding alpha-taxonomy of finless porpoises (although widely accepted at the time) were based on overly-simplified interpretations of results obtained from logically-flawed studies, which were often designed to provide support for the prevailing view of finless porpoise taxonomy, rather than test competing hypotheses objectively. Furthermore, with the exception of P. Wang (37, 38) no objective criteria were used as a metric for making conclusions about taxonomic differentiation and status.

Jefferson (14) conducted the first systematic study of the genus using specimens from virtually the entire range. He examined skull morphometric data, but also addressed other potential differences in coloration and external morphology. Although he declined to make any specific taxonomic revisions at the time, Jefferson's (14) analysis found many significant differences in the skulls of finless porpoises from tropical and temperate portions of the range, with principal components analysis separating his *phocoenoides*-type and *asiaeorientalis*-type specimens (although with some overlap). Because most of his specimens were museum holdings with no availability of information on the form of the dorsal ridge/structure, he was forced to use geographic location as the basis of *a priori* classifications for many of them, as in previous studies. Nonetheless, he found informative differences and suggested that the *phocoenoides*- and *asiaeorientalis*-type porpoises probably represented distinct species. He also

recommended further research, especially focusing on molecular genetics.

Recently, J. Y. Wang et al. (34) published a study that was specifically designed to test the competing hypotheses of a single or multiple species within *Neophocaena* under the definition of the Biological Species Concept (19). Specimens from an area (the Taiwan Strait) where two major morphological forms of finless porpoises are known to be sympatric were the main focus of the study. These specimens were classified independently (and blindly by different researchers) using external morphology and molecular markers (both mtDNA and nuclear DNA). Congruence between their classifications was examined after classifications were finalized. As in all previous studies, two clear external morphological forms with no intermediate forms were found. Structure analysis of nuclear (microsatellite) DNA markers with no *a priori* classification of the specimens also separated them into two clear clusters that were completely congruent with their external morphological forms. Analyses of mtDNA sequences (in the absence of *a priori* classifications) did not reveal any obvious groupings. For both nuclear and mitochondrial DNA, alleles and haplotypes were found to be shared between the two morphological forms. These results were consistent with previous molecular studies; but unlike the other studies, rather than concluding that there was contemporary genetic exchange, J. Y. Wang et al. (34) demonstrated that the shared DNA was due to common ancestry and that exchange of genetic material between the two morphologically-distinct forms probably ended around the last glacial maximum (roughly about 18,000 years ago). In other words, the two morphologically-distinct forms are not interbreeding presently, even where they occur in sympatry, so according to the Biological Species Concept, these two morphological forms are distinct species. The study also suggested that analyses of mtDNA provided insufficient resolution and thus was inappropriate for examining finless porpoise alpha-level taxonomy, because speciation was too recent to allow sufficient time for mtDNA lineages to sort completely. Based largely on these results, the Society for Marine Mammalogy's Taxonomy Committee recently recognized two species of finless porpoises, *N. phocoenoides* and *N. asiaeorientalis*:

http://www.marinemammalscience.org/index.php?option=com_content&view=article&id=420&Itemid=280.

Below we review the evidence for the species split, and in the following section, we provide redescriptions of the two species.

Evidence for Two Species
External Morphology

The main obvious external differences between the two species are found on the dorsal surface as various configurations of the tubercled patch and dorsal ridge. The dorsal surface along the mid-line of the main part of the back of *N. phocaenoides* varies from being flat to concave (the central groove) from where a dorsal ridge may arise as a distinct structure. The dorsal ridge usually appears fairly thick and stiff (not fin-like). At about 75-90% of the length of the body, the ridge or caudal peduncle reaches its apex where it bends ventrally and forms an acute angle. This is seen clearest when viewed laterally (35). The tubercled patch is wide and roughly rhomboidally-shaped, with its posterior end stretching out towards, and onto, the caudal peduncle (Figure 2). There is great individual variability in the shape and position of the tubercled patch. In general, it begins over the thoracic region where it expands quickly to its widest point (varying from about 4 to more than 11 cm and possessing 10-25 longitudinal rows of tubercles) just behind the flippers, before tapering gradually, but obviously, towards the posterior end, where it terminates somewhere on the caudal peduncle. Tubercles are found on top of the dorsal ridge (if present), but can also extend laterally to adjacent areas beyond the ridge (especially near the origin of the ridge). If a distinct ridge is observed on *N. phocaenoides*, it is usually poorly-developed and short, and originates posterior to about mid-back, often appearing as an anterior extension of the caudal peduncle. Lateral grooves are generally not well developed, if present at all.

Within *N. asiaeorientalis*, the presence of central and lateral grooves varies with individuals and geographical locations. If present, the central groove is found anterior to the dorsal ridge and can be bifurcated into lateral grooves by the dorsal ridge. The ridge can begin above the flippers to about mid-way down the

Figure 2 - *External differences between* N. asiaeorientalis *(left and upper) and* N. phocaenoides *(right and lower). Photos by JYW.*

back. The dorsal ridge can be up to 5 cm high and appear as a soft, long-based "fin" on some individuals. The apex of the ridge is usually found at about 50-65% of the body length and is not acutely-angled or pointed like on *N. phocaenoides*, but rather tapers smoothly to the tail stock and thus presents a more rounded profile (35). The tubercled patch is very narrow, varying from about 0.2 to 2.4 cm with 1-10 (more commonly 3-8) longitudinal rows of tubercles across the widest point (7, 8). The general location of the anterior end of the tubercled patch is over the thoracic region, but the exact positions vary greatly. For specimens with ridges arising closer to the head, the tubercles are found on the top of the ridge for more or less the entire length. Whereas, on specimens where the ridge begins near the middle of the back, tubercles run along the midline anterior of the ridge (often in the trough of a central groove) and continue posteriorly onto the top of the ridge, once the ridge begins to appear. The tubercled patch terminates somewhere on the caudal peduncle.

Tubercles have not been observed on the adjacent areas beside the ridge in this species. A plot of the greatest width of the tubercled area vs. the number of rows of tubercles clearly separates out the two species (Figure 3).
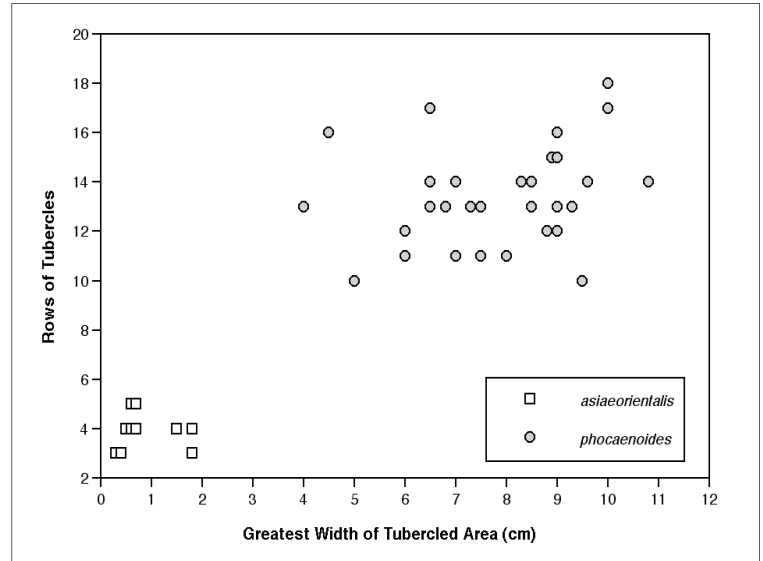

Figure 3 - *Greatest width of the tubercled area vs. number of rows of tubercles for the two species (updated and expanded from 34 - additional data from 8, 13, 23, S. K. Hung, pers. comm., TAJ, unpublished).*

There are also great geographical differences in the maximum size of each of the two species, but in general, the maximum size of *N. phocaenoides* is smaller (maximum known only 171 cm) than for *N. asiaeorientalis* (maximum known up to 227 cm). Note that in the waters of the Matsu Islands, *N. asiaeorientalis* appears to be the smaller of the two species (35). Also, although there have been no quantitative studies, *N. phocaenoides* appears to have a more bluntly rounded forehead than *N. asiaeorientalis*.

Coloration
As adults, the overall coloration of *N. phocoaenoides* is, on average, darker than that of *N. asiaeorientalis*. Interestingly, the later species when found in Japanese waters can be nearly creamy white (16). Calves are born lighter than adults in the former species, while the opposite appears to be true with the latter species. Descriptions of coloration have to be considered cautiously because there are individual, geographical and age-related differences, and

post-mortem color changes (which occur especially rapidly in finless porpoises) can influence characterization of carcasses, while lighting conditions can greatly affect field observations (and photographs) of living animals (35). Nevertheless the light cream color of finless porpoise adults in the northern portions of the range of *N. asiaeorientalis* appears to be unique to this species (Figure 4). In *N. phocoeanoides*, only calves may show a light color approaching this, and adults appear to be much darker gray in all geographic areas so far studied.

Figure 4 - A Japanese finless porpoise in captivity, showing the very light cream color typical of N. asiaeorientalis *from the northern portions of the species' range. Photo with permission by G. Abel/Ocean Park.*

Skull Morphology

    Neophocaena asiaeorientalis specimens have larger skulls, ranging from 209-295 mm, while *N. phocoenoides* specimens have a range of skull lengths of 181-245 mm (14, J. Y. Wang unpublished data). While superficially similar in overall shape, there are several significant differences between the skulls of *phocoenoides*-type and *asiaeorientalis*-type porpoises, and they separated out quite well (although not without overlap) in a principal components analysis (14). In fact, of 25 measurements taken, 21 of them showed statistically-significant differences between the now-recognized species (14). The most obvious difference was in the rostrum, with *asiaeorientalis*-type specimens having a relatively longer and narrower rostrum,

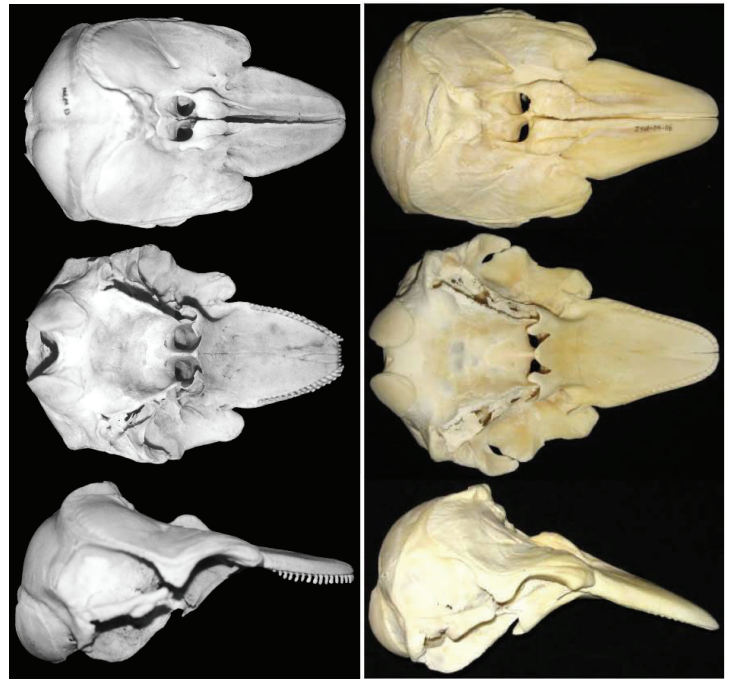compared to the shorter and wider one of *phocoenoides*-type animals (Figure 5).

Figure 5 - Differences in the shape of the cranium between N. phocaenoides *(specimen from Hong Kong, left) and* N. asiaeorientalis *(specimen from the Matsu Islands, right). Both specimens are physically mature. Note the differences in the shape of the rostrum. Photos by TAJ and JYW.*

Molecular Genetics

    Divergence times between the various major forms of finless porpoise have been estimated at 0.37 MYA (39), 0.58-1.08 MYA (42, 43), and 8-18 MYA (7). Although these estimates are widely-divergent, they do all suggest a long history of separation (more than 300,000 years) of the major forms of finless porpoise. However, simulations by J. Y. Wang et al. (34) suggested that the two main forms last exchanged genetic material around the last glacial maximum (about 18,000 years ago) when a land-bridge connecting mainland China to Taiwan (i.e., present-day location of the Taiwan Strait) separated finless porpoises into a temperate form north of Taiwan and a more tropical form to the south. Reproductive isolation in allopatry probably allowed the two forms to differentiate sufficiently so that interbreeding between the two major forms no longer occurs today even in areas where the two forms are sympatric (e.g., in the Taiwan Strait). The

more recent (thousands rather than hundreds of thousands to millions of years) time since divergence of the two main forms was supported by the presence of common mtDNA haplotypes and nuclear alleles in both forms of finless porpoises. The presence of shared mtDNA haplotypes (along with poor study design) has resulted in misinterpretation by researchers, who concluded the presence of contemporary genetic exchange between the two forms (45, 48), rather than incomplete lineage sorting of genetic material retained from sharing a common ancestry (i.e., divergence was too recent to allow fixed genetic differences to be established). The lack of reciprocal monophyly in mtDNA haplotpyes between the two forms was most consistent with a divergence of thousands, rather than hundreds of thousands to millions, of years. The sharing of mtDNA haplotypes and nuclear DNA alleles between the two major forms, as well as animals collected from various geographical regions (including known sympatric waters) was a common result amongst different studies. However, most studies interpreted the shared DNA to mean that contemporary genetic exchange was still ongoing and thus finless porpoises represented a single species with multiple populations or subspecies. In contrast, J. Y. Wang et al. (34) showed that the shared DNA was due to insufficient time since divergence to allow complete lineage sorting that would result in fixed genetic differences. However, reproductive isolation had already developed since the last glacial maximum when the two major groups of finless porpoises were isolated physically from each other. This allowed each group to proceed down a different evolutionary pathway, which is reflected today in their greatly differing external morphologies. The demonstration of reproductive isolation in sympatry provided strong evidence that the two major external forms of finless porpoises represented distinct biological species. Although seasonal shifts in density are known, there is no evidence that either form migrates out of the Taiwan Strait, so the sympatry appears to persist year-round. In further molecular studies of Chinese finless porpoises, Chen et al. (2) concluded that the two-species view was likely correct. However, that study still classified specimens based on collection locations prior to analyses and lacked a theoretical basis for the conclusion of separate species.

Redescription of *N. asiaeorientalis* (Pilleri and Gihr, 1972)

Synonymy

    Delphinus melas Schlegel, 1841
    Neophocaena sunameri Pilleri and Gihr, 1975

    Subspecies nov.
        N. a. asiaeorientalis Pilleri and Gihr, 1972
        N. a. sunameri Pilleri and Gihr, 1975

Holotype and Type Locality

    Skull and postcranial skeleton (MCZ 19998) in the Museum of Comparative Zoology, Harvard University (illustrated in plates 12 and 13 in 23) from the Yangtze River (Kiangsu Prov., Shanghai, P. R. China) (12).

Diagnosis

    This is a relatively-large species of finless porpoise (Figure 6), with total lengths reaching at least 227 cm (36, J. Y. Wang, unpublished data), and adult condylobasal skull lengths ranging from 210 to at least 295 mm (14, J. Y. Wang, unpublished data). The tubercled patch is narrow, between 0.2 and 1.2 cm (occasionally up to 2.4 cm) in width at its widest point (8). The dorsal ridge is high (up to 5.5 cm) and is

Figure 6 - External appearance of N. asiaeorientalis *(dorsal views of two individuals and lateral view). Photos by JYW.*

covered with 1-10 rows of tubercles (7, 8). The ridge originates at or anterior to the mid-length of the dorsum (7). It should be noted that since there was great uncertainty in the taxonomy in the early- to mid-1990s, when the morphological work was conducted (and there was little standardization among researchers in how measurements were taken), the morphological descriptions that were based on these studies need to be viewed cautiously. The skull has a relatively long and narrow rostrum (length ranges from 77-97, with a mean of 86.8 ± 4.88 mm) (14). Twenty-one of 25 skull measurements and meristics showed significant differences from *N. phocaenoides* (14). Tooth counts range from 16-21 in the upper rows and 15-20 in the lower rows (14). Coloration of adults ranges from light cream to dark gray, but in most populations is a moderate shade of gray (53). Newborns are dark gray and lighten as they age (15).

Geographic Variation

There appears to be extensive geographical variation within this species, although this has not been well-documented in most areas. The Yangtze River finless porpoise is considered to be distinct, due to its freshwater habitat (this is the only known wholly-freshwater population of finless porpoise) but there is still some uncertainty about its isolation in the Yangtze River proper (37, 38). It has been recognized for many years as a distinct subspecies, *N. p. asiaeorientalis* Pilleri and Gihr, 1972, and under the two-species arrangement it is renamed *N. asiaeorientalis asiaeorientalis*, while those in coastal marine waters are renamed *N. a. sunameri* Pilleri and Gihr, 1975. The Yangtze finless porpoise with a maximum known length of 177 cm is smaller than the subspecies found in marine waters. Its dorsal ridge rarely exceeds 1.5 cm in height, and has only 1-5 rows of tubercles. It is dark gray, much darker in color than *N. a. sunameri* from the waters of northern China, Korea, and Japan, all of which are a lighter gray to cream color as adults (26, 53). Thus far, no studies have documented differences in the finless porpoises from the Yellow/Bohai seas and Korea from those in Japanese waters, but the Korea Strait appears to be an area of absence (30) and may represent a barrier to exchange between animals of Chinese-Korean waters and those in Japanese waters, albeit

possibly an incomplete one (52, J. Y. Wang, unpublished data). Within Japanese waters, five distinct and isolated populations have been suggested based on differences in skull morphology and molecular genetics (49, 50, 51).

Distribution, Habitat and Ecology

This species is known from temperate coastal waters of the western Pacific Ocean, from the Taiwan Strait northwards to Korea and central Japan (Sendai Bay), including the middle and lower reaches of the Yangtze River (Figure 7). A recent discovery of an emaciated and severely compromised (died shortly after retrieval) individual from Okinawa Island, Japan (52) is likely an extralimital record of this species. The known range includes Japanese, Korean, Chinese (including Taiwanese) waters. It is believed that the nominate subspecies is found exclusively in the Yangtze River, while *N. a. sunameri* is found in coastal marine and estuarine waters.
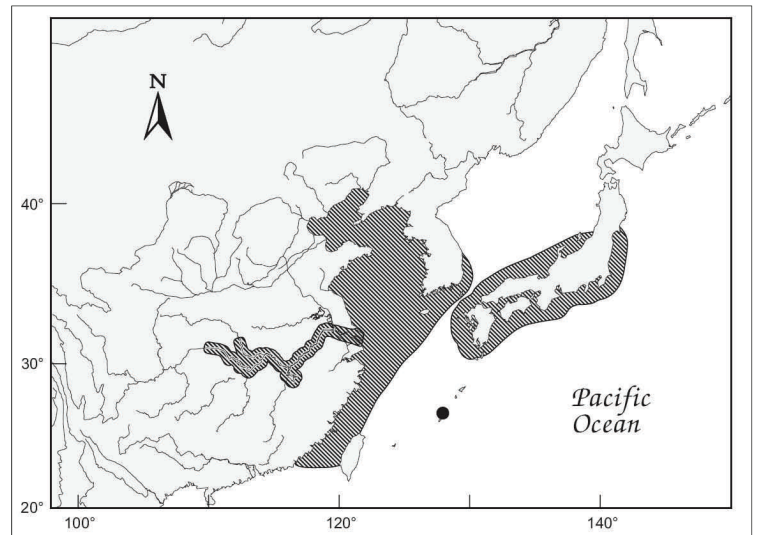

Figure 7 - Range map of N. asiaeorientalis. *Extralimital record from Okinawa (52) is also shown as a black dot.*

For this species, the calving season appears to be mostly in the spring to summer months of March to August, although the populations around the island of Kyushu, Japan, apparently have their calving peak in winter months, November to December (55).

Suggested Common Names

Narrow-ridged finless porpoise (to reflect its unique dorsal structure, which clearly distinguishes it

from *N. phocaenoides*).

Subsp. *asiaeorientalis* – Yangtze finless porpoise
Subsp. *sunameri* – East Asian finless porpoise

Conservation Status

Because fisheries-related mortality occurs throughout the range of this species and is suspected to be unsustainably high in some regions and there is evidence of large declines for some populations (e.g., the Yangtze River subspecies, the Inland Sea of Japan population), observations of population reductions in many parts of its range, a decline of at least 30% over the last three generations was suspected or inferred. Under the criteria of the IUCN Red List of Threatened Species, this species was assessed to be Vulnerable (VU A2cde – 32).

Redescription of *N. phocaenoides* (G. Cuvier, 1829)
Synonymy

Delphinapterus molagan Owen, 1866
Neomeris kurrachiensis Murray, 1884

Holotype and Type Locality

Skull (originally "with skin" - MNHN A-3086) in the Museum National d'Histoire Naturelle, Paris, is illustrated in figures 11 and 12 of that manuscript (28). The oft-cited type locality of the Cape of Good Hope is now considered erroneous (14, 27). Robineau (28) conducted an extensive investigation of this issue and concluded that the type specimen in fact almost certainly came from the Malabar coast (India), which is well within the known range of this species.

Diagnosis

This is the smaller of the two species of finless porpoise (Figure 8), reaching a known maximum total length of only 171 cm. Adult condylobasal skull length ranges from 181 to 245 mm (14). The dorsal structure (often variously called a "ridge" or "groove" in the literature) is low and wide, ranging from 4.8-12.0 cm in width, with 10-17 (occasionally as few as 9 or up to 25) roughly-longitudinal rows of tubercles (7, 8, 23). Even in calves, the dorsal structure is wider than in adults of *N. asiaeorientalis*, from about 3.1-6.0 cm (24, Jefferson unpublished data). The ridge begins posterior to the mid-length of the body (7). The skull has a rostrum that is
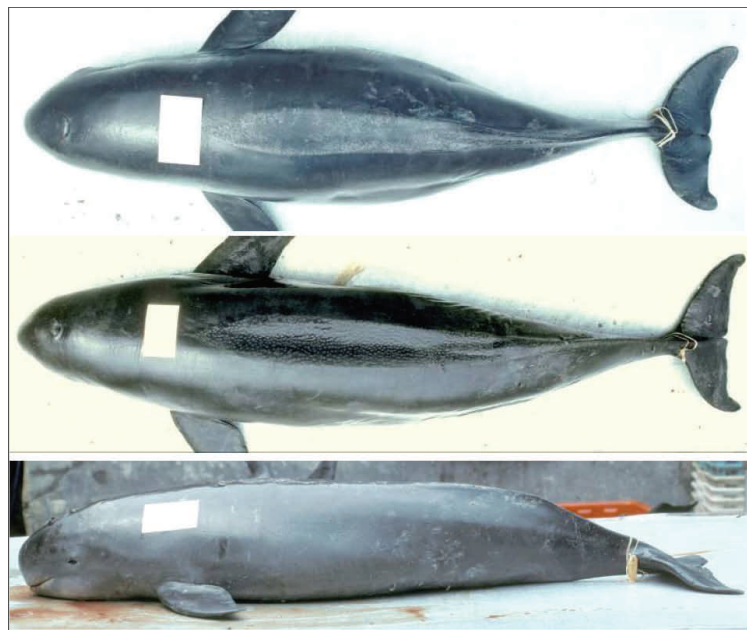

Figure 8 - External appearance of N. phocaenoides *(dorsal views of two individuals and lateral view). Photos by JYW.*

relatively wide and short; its length ranges from 62-92 and a mean of 74.6 ± 7.62 mm (14). Of 25 skull measurements and meristics, significant differences from *N. asiaeorientalis* were found in 21 (14). Tooth counts range from 15-22 in the upper rows and 16-22 in the lower rows (14). Adult coloration is dark gray to nearly black, though newborns are much lighter than adults, often a creamy gray (15).

Geographic Variation

Extensive geographical variation also exists in this species, although very few specimens from the Indian Ocean portion of the range have been reported in the literature. Specimens of *N. phocaenoides* from the northern and southern South China Sea appear to be distinguishable based on size, with the northern form being much larger (documented CBL = 209-245 mm) than the southern form (CBL = 181-208 mm) (14). They also separated out well in a principal components analysis (14). Specimens from the Indian Ocean appear to be separate from those in the South China Sea, based on the depth of the pterygoid notch (measured specimens from the Indian Ocean have been < 14 mm and most from the South China Sea have been > 14 mm) (14). There are also reported coloration differences in the Indian Ocean, with light patches on the underside of the head and chest, although these have not been well-

documented with large sample sizes (23). Presently, no subspecies are recognized within this species.

Distribution, Habitat and Ecology

This finless porpoise species is found in shallow tropical and subtropical waters of the Indian Ocean and Southeast Asia, from the Persian (Arabian) Gulf eastwards around the coastal rim to at least the Taiwan Strait (to approximately 25°N – Figure 9). A record of this species from the Yellow/Bohai Sea region (37, 38) was likely an extralimital event, but it does suggest that the present accepted northern limit for this species (i.e., the waters of the Matsu Islands) may be too far south. The known range includes the waters of China (including the Special Administrative Regions of Hong Kong and Macau), Taiwan, Vietnam, Cambodia, Thailand, Brunei, Malaysia, Singapore, Indonesia, Myanmar (=Burma), Bangladesh, India, Sri Lanka, Pakistan, Iran, Iraq, Kuwait, Saudi Arabia, Qatar, the United Arab Emirates and Bahrain (15). Presently, the species has not been confirmed from the waters of Oman and the Philippines, but may be expected to occur in these locations. However, in the Philippines it may only occur in restricted parts of the country, and appears to be absent from most Philippine marine waters (4, 5, 22).
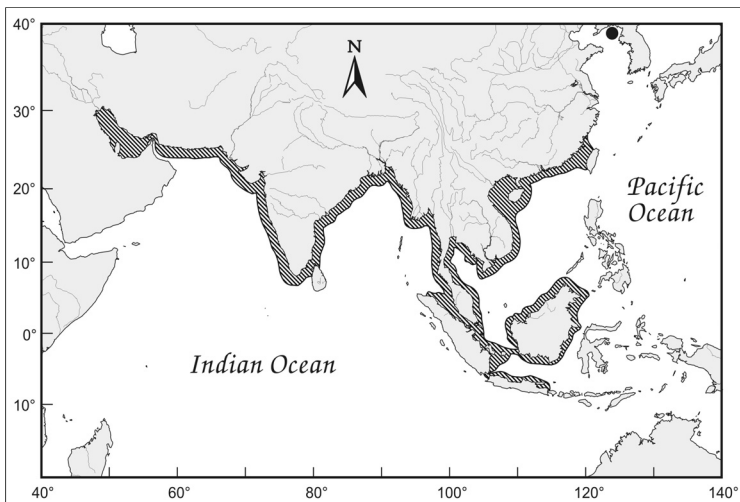

Figure 9 - Range map of N. phocaenoides. *Extralimital record from Yellow/Bohai Sea region (37, 38) is also shown as a black dot.*

Calving in this species has not been well studied in most areas. Most information is from the region of Hong Kong and southern China. There appears to be a rather protracted calving season (June to March), which is not unexpected in a species such as this that has a tropical/subtropical habitat. In Hong Kong, where the species has been studied most intensively, the peak in calving is in late autumn to winter months of October to January (55).

Suggested Common Name

Indo-Pacific finless porpoise (to reflect its main distribution in tropical to subtropical waters of the Indian Ocean and western Pacific Ocean).

Conservation Status

Because fisheries-related mortality occurs throughout the range of this species and is suspected to be unsustainably high in some regions and there are observations of population reductions in many parts of its range, a decline of at least 30% over the last three generations was suspected or inferred. Under the criteria of the IUCN Red List of Threatened Species, this species was assessed to be Vulnerable (VU A2cde) (33).

Conclusions

The evidence reviewed above makes it clear that there are at least two species of finless porpoises. Those with a wide dorsal tubercled area and dark adult coloration occur in more tropical portions of the range of the genus and are referable to *Neophocaena phocaenoides*. Finless porpoises with a narrow dorsal ridge and more variable adult coloration (some being very light in color) are found in the more temperate portions of the range and represent the species *Neophocaena asiaeorientalis*. Each species displays extensive geographical variation (much of it not yet well documented), and it is clear that multiple geographic forms are present within each. Further taxonomic work should show whether these should be treated simply as un-named geographic forms, subspecies, or possibly even additional species.

As with taxonomic investigations of just about any wide-ranging marine mammal, much more of the range needs to be studied to determine if other species exist, as well as to understand intraspecific divisions within the species. Multiple characters should be examined, including morphology (osteological and external) and

molecular markers (mtDNA, as well as various nuclear markers). Standardization of methodology and terminology would improve the efficacy of future taxonomic studies. Ecological and demographic information is also likely to shed some light on the taxonomy of these animals, especially at the intraspecific level. Further standardization of research methodologies (e.g., characters to measure and how to measure them) will be very important for useful comparisons across regional studies. And finally, well designed studies based on an appropriate species/subspecies concept are crucially important for addressing the taxonomic questions of interest.

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