PRELIMINARY ANALYSIS OF GEOGRAPHIC VARIATION IN CRANIAL MORPHOMETRICS OF THE FINLESS PORPOISE (*NEOPHOCAENA PHOCAENOIDES*)

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ABSTRACT. – The taxonomy of the finless porpoise (*Neophocaena phocaenoides*), while better-studied than that of many species of small cetaceans, still suffers from some uncertainties and a general lack of data from most of the range. In this study, skull morphometric and meristic data were collected from 218 specimens from throughout the range of the species. Bivariate and multivariate Principal Components Analyses (PCA) were used to examine the sample for geographic variation. Results indicated that there is a great deal of geographic variation in the size and shape of skulls of porpoises from different areas. The two primary types of finless porpoise found in tropical and temperate waters showed some separation in both the PCA and rostrum shape analyses (but with some overlap in all features analyzed). However, there was not strong support from skull morphology for their distinctness at the species level. The temperate form, *asiaeorientalis*-type, is found in coastal and riverine waters of Japan, Korea, and northern China. It is relatively large (total length up to 227 cm and adult CBL 209-251 mm), with a narrow dorsal ridge (< 1.3 cm), a relatively narrow rostrum, and adult coloration ranging from black to light gray. The tropical form, *phocaenoides*-type, occurs in the Indian Ocean (including the Persian Gulf) and South China Sea. Some populations of the latter are small (perhaps not exceeding 160 cm total length), and adult CBL ranges from 181-245 mm. It has a wide dorsal ridge (> 3.4 cm), relatively wide rostrum, and dark-gray adult coloration. Two geographic populations were recognized within the *asiaeorientalis*-type, and three within the *phocaenoides*-type. Further work, especially analyses of skulls from unstudied portions of the range, systematic studies on dorsal ridge width, and molecular genetics, are needed to clarify taxonomic relationships and to identify stocks for management.

KEY WORDS. – Finless porpoise, *Neophocaena phocaenoides*, taxonomy, systematics, geographical variation, skull morphology, osteology.

INTRODUCTION

The finless porpoise *Neophocaena phocaenoides* (G. Cuvier, 1829) is distributed throughout the coastal waters of the Indo-Pacific region, from southern Japan in the east to the Persian Gulf in the west (Reeves et al., 1997; Kasuya, 1999). A number of taxonomic investigations have been performed on these animals, and the taxonomic history of the genus is rather complicated (see review in Kasuya, 1999). Overall, five species have been described (see Appendix A), and the first focussed taxonomic work suggested that the genus should be divided into three species: *N. phocaenoides* in the Indian Ocean, *N. asiaeorientalis* in the Yangtze River of China, and *N. sunameri* in Korean and Japanese waters (Pilleri & Gihr, 1972, 1975; Pilleri & Chen, 1980).

There seems to be little doubt that the Indian Ocean form is distinct from the Far East forms, as there are apparently clearcut morphometric differences between it and the other two, especially in the region of the pterygoid hamuli (see

Fraser, 1966). However, van Bree (1973) suggested that the differences between the Japanese and Chinese animals were taxonomically insignificant. Gao & Zhou (Gao, 1991; Gao & Zhou, 1995a, b, c) have done the most careful and comprehensive systematic work to date. They confirmed that the three forms described as species by Pilleri & Gihr (1972, 1975) were in fact distinct, but suggested that the differences were of a subspecific, rather than a specific, nature. This basic systematic arrangement has been supported by additional studies (Wang et al., 1989; Wang, 1992a, b; Amano et al., 1992). Thus the genus *Neophocaena* is currently thought to be monospecific, with three subspecies recognized (Rice, 1998). These are *N. p. sunameri* Pilleri & Gihr, 1975, which occurs from the East China Sea to southern Japan; *N. p. asiaeorientalis* (Pilleri & Gihr, 1972), which is found only in the Yangtze River of China; and *N. p. phocaenoides* (G. Cuvier, 1829), which has an extensive distribution from the South China Sea to the Persian Gulf. *Neophocaena p. sunameri* and *N. p. asiaeorientalis* both have a narrow dorsal ridge (<1.3 cm), while *N. p.*

phocaenoides has a much wider dorsal ridge (>2.9 cm). The recent work of Yoshida et al. (1995), using multivariate statistical analyses of a large sample of skulls from Japan, found evidence for five populations of *N. p. sunameri* in Japanese waters. That study demonstrated the potential for revealing stock or population-level differences in careful studies with adequate samples and modern analysis techniques.

Although the above arrangement is widely accepted, there are many remaining problems that result in uncertainties in the taxonomy of this genus. First, nearly all of the specimens used in previous taxonomic studies have come from China and Japan, which together represent only a small part of the overall range. The main exceptions to this are the studies of Pilleri & Gihr (1972, 1975), which included a small sample of specimens from Pakistan (but suffered from methodological problems); and the work of Amano et al. (1992), which included information from a few other locations in the Indian Ocean. However, in the latter study, the authors used data from publications by other workers (thereby introducing inter-observer variability as a potential confounding factor), and the sample sizes from most sections of the range were still very small.

Information in the literature indicates that finless porpoises from any specific area have either a narrow (0.2-1.2 cm) or a wide (3.0-12.0 cm) dorsal ridge, depending on the area. For instance, finless porpoises from the Yangtze River have dorsal ridges of 0.2-0.8 cm wide (n = 39 - Gao and Zhou, 1995a) and those from the Yellow Sea have ridges of 0.2-1.2 cm (n = 77 - Gao and Zhou, 1995a). Additionally, although there appear to be no published data available, porpoises from Japan also have relatively narrow dorsal ridges. On the other hand, porpoises from the northern South China Sea have ridges of 4.8-12.0 cm (n = 42 - Gao and Zhou, 1995a), Hong Kong specimens have ridges of 3.5-12.0 cm (n = 26 - Parsons and Wang, 1998; Jefferson, unpubl.), Thailand 3.5-6.0 cm (n = 4 - Pilleri and Gihr, 1974), and Pakistan 4.2-5.4 cm (n = 5 - Pilleri and Gihr, 1974). The only area known to have both wide-ridge and narrow-ridge finless porpoises is the Taiwan Strait along the mainland coast of Fujian Province, and possibly the East China Sea. There, although sample sizes are small, porpoises of both types have been examined, but all specimens appear to fall neatly into one or the other category. For instance, Huang et al. (2000) examined four narrow-ridge specimens (0.4-0.6 cm) and 17 wide-ridge specimens (3.0-9.5 cm), all collected from the same fishing port. It would thus appear that there might be two distinct forms (or species) of the finless porpoise, differing in the width of the dorsal ridge. Of course, there are other possible explanations (e.g.,
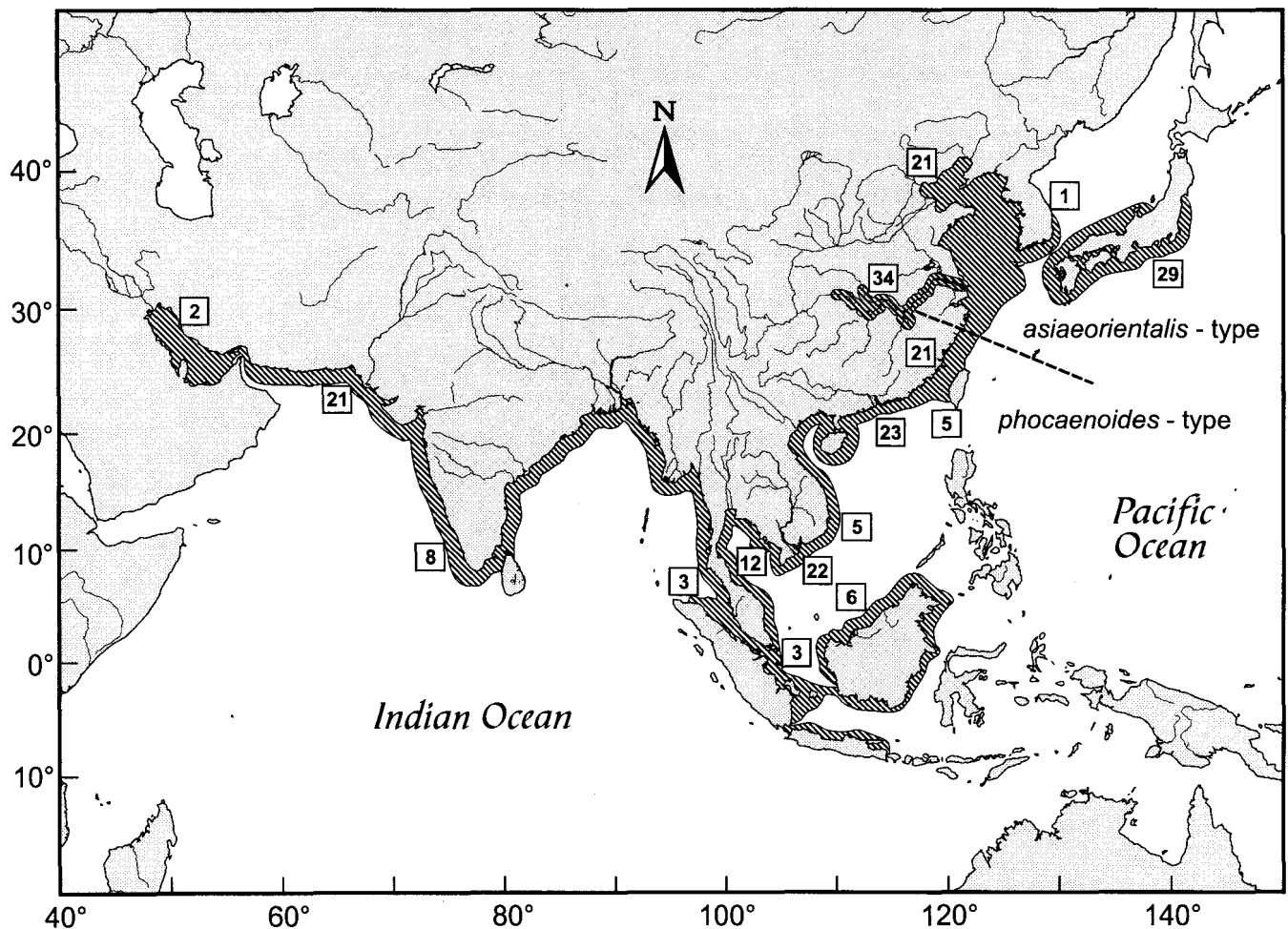

Fig. 1. Map of the suspected range of the finless porpoise, showing locations where the specimens used in this study were collected. Sample sizes of measured skulls are shown by numbers in the boxes. The dashed line indicates the geographical separation of *asiaeorientalis*-type and *phocaenoides*-type specimens used in this study.

seasonal migrations of two intraspecific forms, or current sample too small to include intermediates).

There clearly remains a need for a re-examination of the geographic variation and taxonomy within the species, which includes a large sample of data from throughout a representative portion of the overall range and eliminates inter-observer variability as an issue. The present study is intended to fill this need.

MATERIALS AND METHODS

Data Collection
Morphometric and meristic data were collected from finless porpoise skulls from throughout the entire range, which were deposited in various museums, research institutes, whale temples, and a few personal collections. The database consisted of data from 218 specimens: 2 from the Persian Gulf, 21 from Pakistan, 8 from India, 3 from the Thai Andaman Sea, 12 from the Gulf of Thailand, 3 from Singapore, 6 from Borneo, 22 from the Mekong River Delta, 5 from southcentral Vietnam, 23 from Hong Kong, 21 from Fujian Province, China, 5 from Taiwan, 34 from the Yangtze River, 21 from the Yellow/Bohai seas, 1 from Korea, 29 from Japan, and 2 from unknown locations (Fig. 1; Appendix B). The measured sample included the holotype specimens of *Delphinus phocaenoides* G. Cuvier, 1829; *Delphinus melas* Schlegel, 1841; *Neomeris asiaeorientalis* Pilleri & Gihr, 1972; and *Neophocaena sunameri* Pilleri & Gihr, 1975. Measurements were taken with an anthropometer (a type of

vernier calipers) and, in some cases, dial calipers. Most measurements were taken to the nearest millimeter, but measurements of less than 10 mm were taken to the nearest 0.1 millimeter. All measurements and counts were taken by the author, thereby eliminating the potential problem of inter-observer bias.

Measurements and meristics taken were a subset of those used by Perrin (1975), but with the addition of three measurements: length of the mandibular symphysis, depth of pterygoid notch, and tooth diameter (Table 1, Fig. 2). The 22 measurements were chosen to characterize functional elements of the odontocete skull, such as the feeding apparatus and the sound production apparatus. For tooth counts (greatest upper and lower tooth counts), the higher count between right and left sides was used in analyses (after Amaha, 1994). Museum and collection acronyms are given in Appendix C.

Table 1. List of measurements and meristics taken on finless porpoise skulls.

Character	Number#	Abbreviation
Condylobasal Length	1	CBL
Length of Rostrum	2	LRO
Width of Rostrum at Base	3	WRB
Width of Rostrum at 1/2 Length	5	WRH
Width of Rostrum at 3/4 Length	7	WRT
Width of Premaxillae at 1/2 Length	6	WPH
Greatest Width of Premaxillae	15	GWPM
Preorbital Width	10	GPRW
Postorbital Width	11	GPOW
Zygomatic Width	14	GWZP
Parietal Width	16	PARW
Width of External Nares	13	GWEN
Width of Internal Nares	27	GW
Length of Temporal Fossa	19	LTF
Height of Temporal Fossa	20	HTF
Length of Orbit	25	LOR
Length of Antorbital Process	26	LAPL
Length of Upper Toothrow	32	LUTR
Length of Mandible	38	LMAN
Height of Mandible	39	HMAN
Length of Mandibular Symphysis*	—	LMSY
Depth of Pterygoid Notch*	—	DOPT
Greatest Upper Tooth Count	33/34	UTC
Greatest Lower Tooth Count	35/36	LTC
Tooth Diameter (middle lower left)*	—	TD

\# Following Perrin (1975).
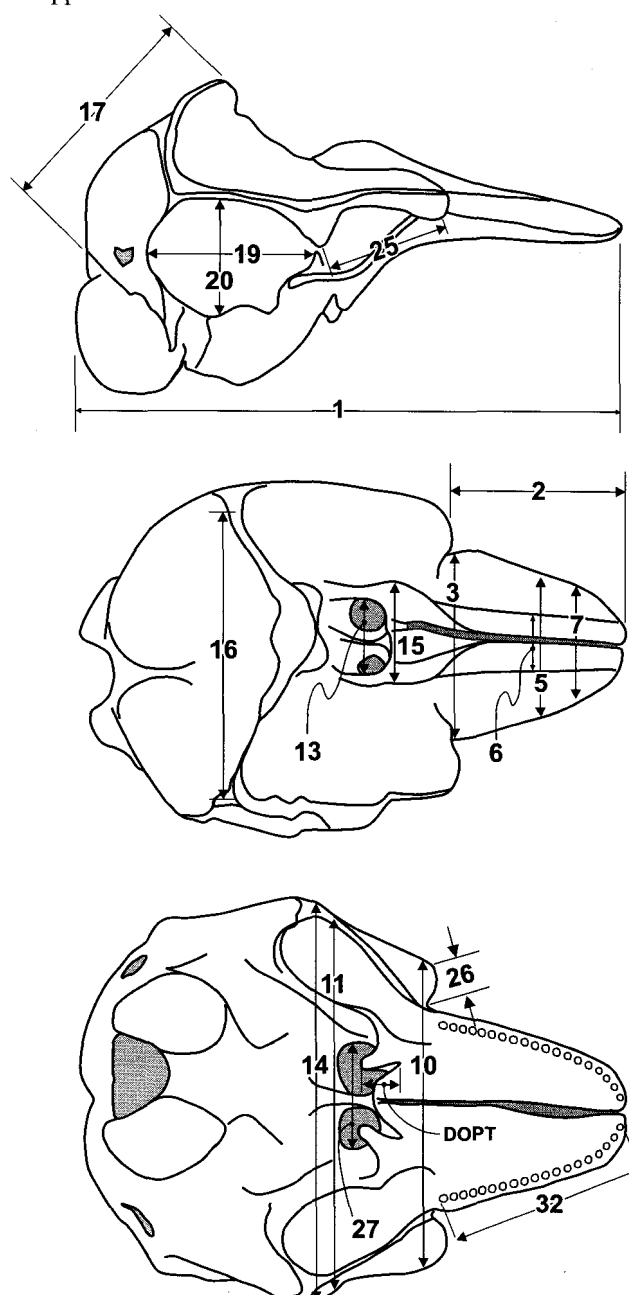* These measurements were not taken by Perrin (1975).

Fig. 2. Schematic diagram showing measurements taken on finless porpoise skulls. Refer to Table 1 for a list of measurements.
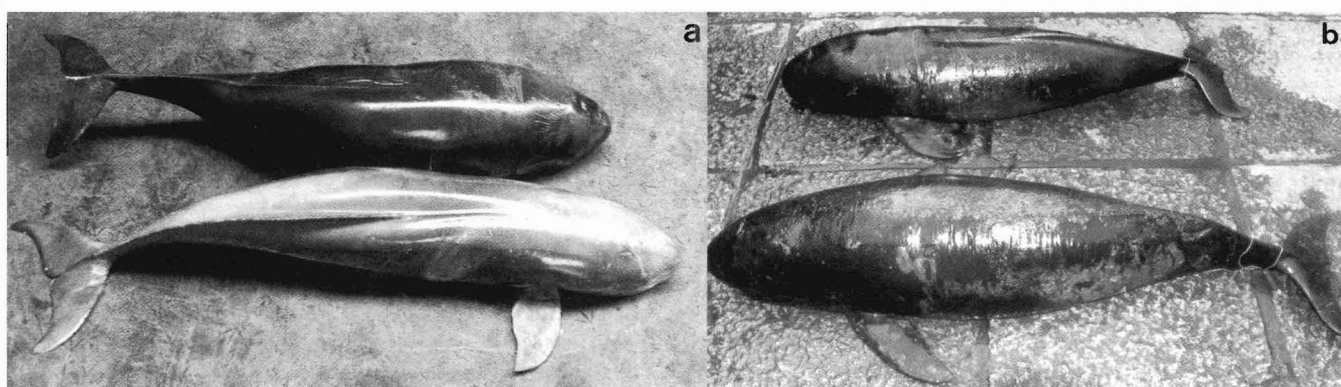
Fig. 3. Variation in external morphology and coloration of finless porpoises from Chinese waters. The left photo (a) shows two *asiaeorientalis*-type finless porpoises captured near the mouth of the Yangtze River: 120 cm female with dark coloration (top), and 121 cm female with light coloration (bottom - photo courtesy of Zhang Xianfeng). The right photo (b) shows two adult-sized porpoises captured in southern Fujian Province, near Xiamen: *asiaeorientalis*-type specimen with dark coloration and narrow ridge (top), and *phocaenoides*-type porpoise with dark coloration and wide dorsal ridge (bottom - photo courtesy of the late S. Leatherwood).

Statistical Analyses

Each specimen was divided into one of three groups, based on its geographic origin and/or information on dorsal ridge width:

(1) *asiaeorientalis*-type (Figs. 3a, b, 4a) — This group was composed of specimens from the more temperate portions of the range: the Yangtze River, Yellow/Bohai seas, and Japan, and included specimens currently recognized as *N. p. sunameri* Pilleri & Gihr, 1975 and *N. p. asiaeorientalis* (Pilleri & Gihr, 1972).

Although dorsal ridge data were not available for all specimens, the literature clearly indicates that specimens from these areas have narrow dorsal ridges (0.2-1.2 cm wide with 2-10 rows of denticles) (Wang, 1992a, b; Gao & Zhou, 1995a, b, c; Mizue et al., 1965).

(2) *phocaenoides*-type (Figs. 3b, 4b) — This group was made up of specimens from the more tropical areas (e.g., Taiwan, the South China Sea, and the Indian Ocean), which included specimens now classified as *N. p. phocaenoides* (G. Cuvier, 1829). All specimens with dorsal ridge data had a relatively wide dorsal ridge (3.0-12.0 cm wide with 10-25 rows of denticles), and the literature indicates that specimens from these areas always have a wide ridge (Pilleri & Gihr, 1974; Pilleri & Chen, 1980; Wang, 1992a, b; Gao & Zhou, 1995a, b, c; Parsons & Wang, 1998; Jefferson & Braulik, 1999). The only exception is the mainland coast of the Taiwan Strait, which is known to contain specimens of both narrow and wide dorsal ridge widths (Huang et al., 2000). For the 21 specimens from that area of Fujian Province, 19 of them had wide ridges (A. Gao, pers. comm.) and were thus assigned to the *phocaenoides*-type.

(3) Unknown type — There were four specimens that could not be reliably associated with either type. This included two specimens from the Taiwan Strait (where both forms appear to occur), which had no associated data on dorsal ridge width, as well as two other specimens from unknown localities (i.e., they could have come from the Taiwan Strait as well) and no ridge width data.
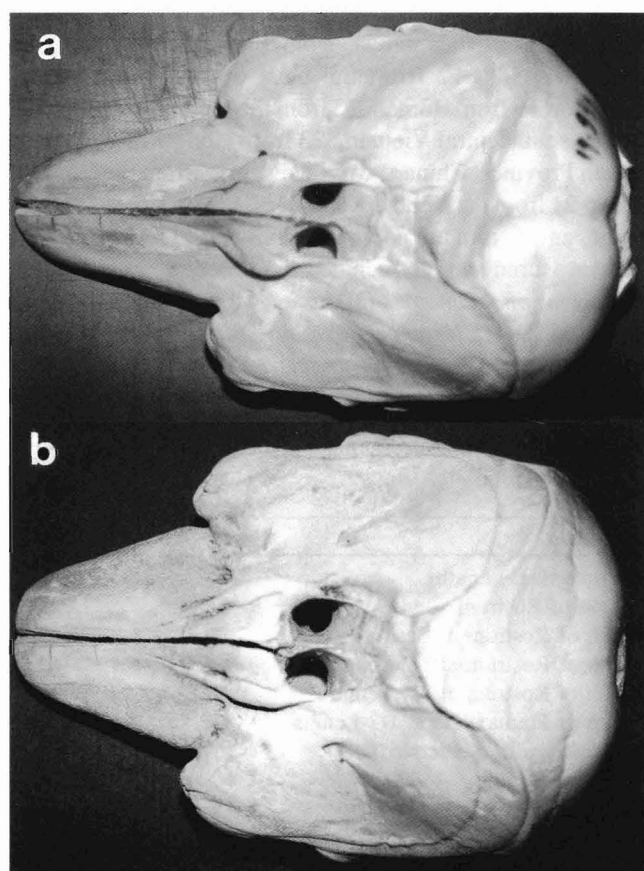

Fig. 4. Variation in shape of rostrum of finless porpoises skulls, showing the extremes of variation in shape of the rostrum. An *asiaeorientalis*-type skull from Japan (ZMA 17.942), with a rostrum length/width at base ratio of 1.37 (a). A *phocaenoides*-type skull from Hong Kong (OPCF NP99-16/07), with a rostrum length/width at base ratio of 1.01 (b).

Further, specimens of each of the two main types were divided into groups based on their geographic origin. The *asiaeorientalis*-type specimens, were divided into groups from Japan (including the one specimen from Korea), the Yangtze River, and the Yellow/Bohai seas. The *phocaenoides*-type animals were divided into northern South China Sea (southcentral Vietnam, Hong Kong, Fujian Province, and Taiwan), southern South China Sea (Gulf of

Thailand, Singapore, Borneo, and Mekong River delta), and Indian Ocean (Persian Gulf, Pakistan, India, and Thai Andaman Sea) groups.

Multivariate statistics, which are generally recognized to have higher analytical power than univariate statistics, were used to examine the sample for evidence of geographical variation. I used the entire dataset in most analyses, including specimens of unknown type. Principal Components Analyses (PCA) were conducted using the statistical software, STATISTICA® For the Macintosh v4.1 (StatSoft, 1994). To be included in analyses of geographical variation, each skull had to be intact (e.g., the rostrum and brain case could not be missing significant portions), and to be considered cranially adult (i.e., the major bones of the skull had to be fully fused). Data on sexual maturity and physical maturity, when available, were used as indicators of cranial maturity. There is no distal rostral fusion of adults in this species, as occurs in some dolphin species. Because there was no foolproof way to ensure that any specific skull had stopped growing, and biological data were not available for

all specimens, it is possible that development variation could affect the results. However, I believe that any such effect is minimal.

Multivariate analyses are known to be sensitive to missing data. Therefore, measurements were excluded if data were missing from more than 5 specimens. For the remaining measurements with incomplete data, missing values were estimated using the mean substitution method available in STATISTICA. All statistical tests were conducted at alpha = 0.05.

RESULTS

Differences Between the Two Types
On average, the skull of the *phocaenoides*-type is smaller than that of the *asiaeorientalis*-type, and in general, specimens from more tropical areas tend to be smaller than those from more temperate regions (Fig. 5). Specimens from India and Pakistan appear to be even smaller that would be expected based on their latitudes. However, when one examines a boxplot of condylobasal length for the specimens of the two types, it becomes clear that while the *asiaeorientalis*-type is relatively large, specimens of the *phocaenoides*-type from different areas are highly variable in size (Fig. 5). The larger specimens of both types (e.g., those from southcentral Vietnam, Hong Kong, Taiwan, Fujian Province, the Yangtze River, Japan, and the Yellow/ Bohai seas) show extensive overlap in size.

A Principal Components Analysis was performed on a sample of 165 skulls (65 *asiaeorientalis*-type, 98 *phocaenoides*-type, and 2 unknown-type skulls). Eleven characters with a minimum of missing values were analyzed (upper tooth count, condylobasal length, length of rostrum, width of rostrum at base, preorbital width, parietal width, width of external nares, height of temporal fossa, length of orbit, length of antorbital process, and length of upper tooth row). Two principal components were extracted, with PC1 and PC2 explaining 53.3% and 14.4% of the variance, respectively. The factor loadings are shown in Table 2.
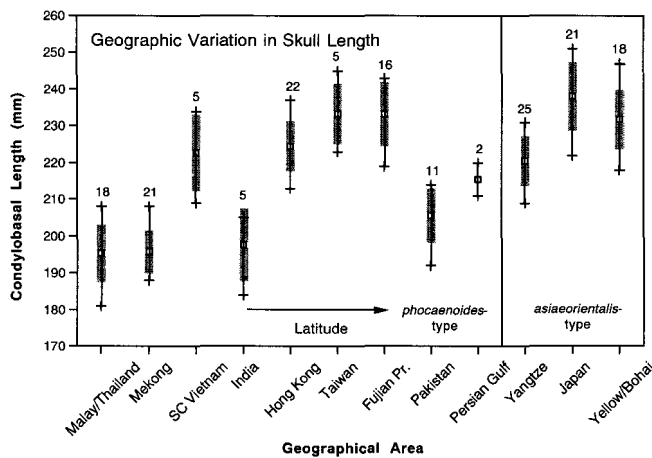

Fig. 5. Boxplot of condylobasal length for finless porpoise skulls from different areas of the species' range. Latitude increases from left to right. The center points are the means, vertical bars are the ranges, shaded boxes are standard deviations, and numbers above are sample sizes.

When the first two principal components data were plotted, the results showed a high degree of separation of the two types, but there was some overlap (Fig. 6). The two types showed the most separation on PC2, which presumably represents skull shape. There was similar separation of the two types on a plot of length of rostrum vs. width of rostrum at base (Fig. 7). The relatively narrow rostra of the *asiaeorientalis*-type specimens showed only a small degree of overlap with the relatively wider rostra of the *phocaenoides*-type specimens. Only 13 of 166 (7.8%) of the specimens occurred in, or on the border of, the area of overlap. The two specimens of unknown type did not occur in the area of overlap in Figures 6 or 7. Both grouped with the *phocaenoides*-type specimens in the PCA (Fig. 6). However, in the rostrum shape analysis (Fig. 7), one specimen was outside both clusters (although in an area that would probably be associated with the *phocaenoides*-type),
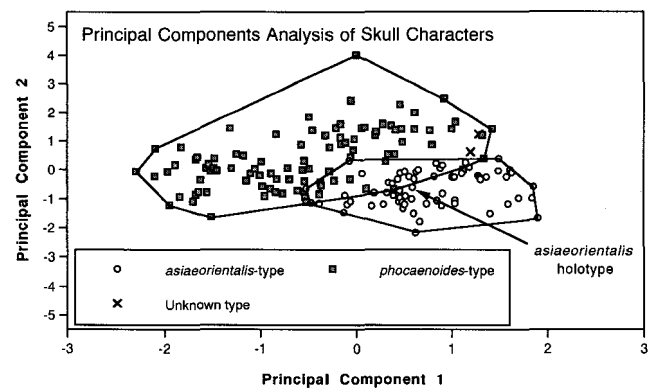

Fig. 6. Scatterplot of first and second PCA scores for *asiaeorientalis*-type and *phocaenoides*-type specimens. The holotype of *N. asiaeorientalis* is shown, but the *N. phocaenoides* holotype was considered to be a subadult, and so was not used in the PCA.

Table 2. Factor loadings for the two principal components (after quartimax rotation).

Character	Factor 1	Factor 2
Upper Tooth Count	0.1583	-0.1187
Condylobasal Length	0.9162	0.2370
Length of Rostrum	0.9350	0.0246
Width of Rostrum at Base	0.5274	0.7006
Preorbital Width	0.7868	0.4200
Parietal Width	0.7458	0.4393
Width of External Nares	0.1409	0.8172
Height of Temporal Fossa	0.5963	0.0816
Length of Orbit	0.3817	0.7521
Length of Antorbital Process	0.7861	-0.2904
Length of Upper Toothrow	0.9226	0.0947
Variance	0.4711	0.2059

and the other one grouped with the *asiaeorientalis*-type specimens.

Means and associated parameters for measurements and meristics of the two forms are given in Table 3. Means of width of rostrum at base, width of rostrum at 1/2 length, width of premaxillae at 1/2 length, width of external nares, and greatest lower tooth count were significantly larger for the *phocaenoides*-type. The following characters were larger for the *asiaeorientalis*-type: condylobasal length, length of rostrum, greatest width of premaxillae, preorbital width, postorbital width, zygomatic width, parietal width, length of temporal fossa, height of temporal fossa, length of antorbital process, length of upper toothrow, length of mandible, height of mandible, length of mandibular symphysis, depth of pterygoid notch, and tooth diameter.

Geographic Variation Within Each of the Two Forms
To examine for further potential geographic variation, a separate PCA was conducted for each type (Fig. 8). The PCA for the *asiaeorientalis*-type specimens involved three geographical areas (e.g., Japan, Yangtze River, and Yellow/Bohai seas). A total of 66 specimens were analyzed (21 from Japan, 27 from the Yangtze, and 18 from the Yellow/Bohai seas). Three principal components were extracted; PC1 summarized 44.1% of the total variation, and PC2 summarized 16.5%. The analysis showed only partial separation, with each population strongly overlapping the other two (Fig. 8a).

The PCA for the 112 *phocaenoides*-type specimens also involved three geographical groups (24 from the Indian Ocean, 49 from the northern South China Sea, and 39 from the southern South China Sea). Two principal components were extracted. The first component accounted for 64.6% and the second component 11.5% of the variation. While the Indian Ocean specimens overlapped with both the other two proposed forms, there was almost complete separation of the northern and southern South China Sea specimens on the PC1 axis (Fig. 8b). Principal Component 1 appears to represent skull size, and there was no overlap in the ranges of condylobasal lengths of specimens from northern and southern South China seas (Fig. 9). The more northern specimens from the South China Sea (209-245 mm) were
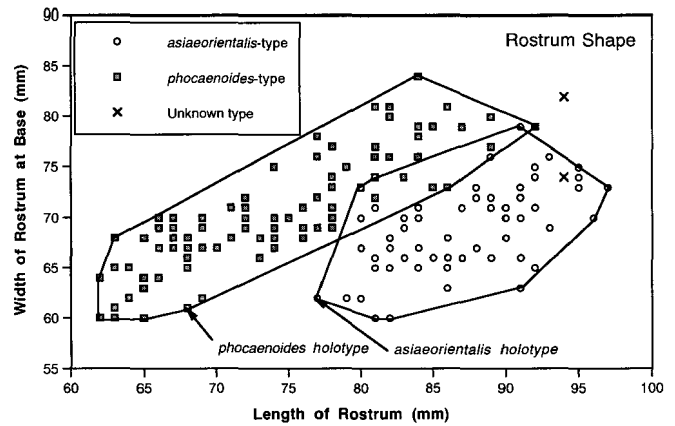

Fig. 7. Scatterplot of length of rostrum vs. width of rostrum at base for *asiaeorientalis*-type and *phocaenoides*-type specimens.
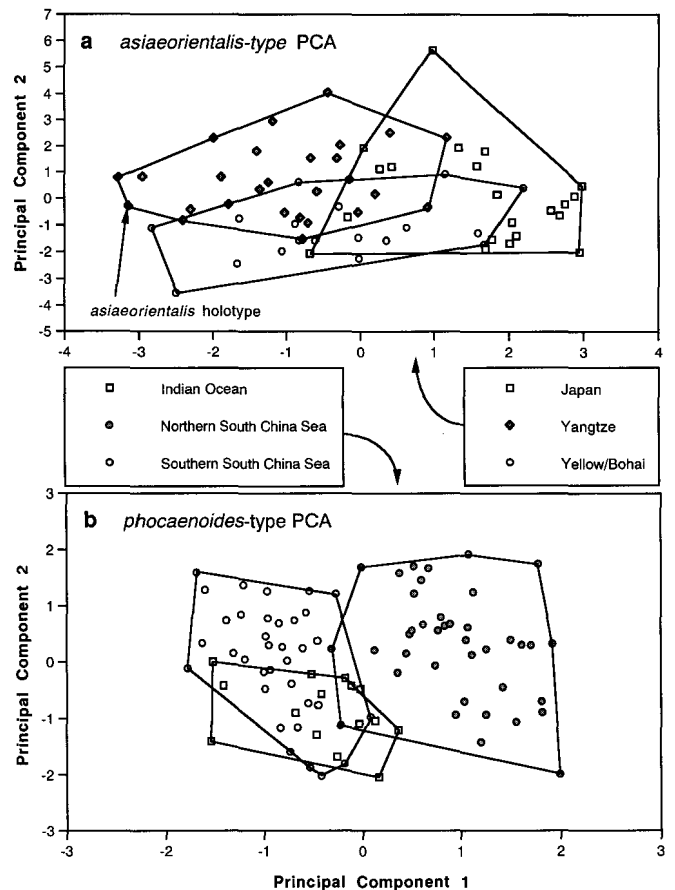

Fig. 8. Scatterplot of first and second PCA scores for *asiaeorientalis*-type specimens (a) and *phocaenoides*-type specimens (b). The holotype of *N. asiaeorientalis* is shown, but the *N. phocaenoides* holotype was considered to be a subadult, and so was not used in the PCA.

on average much larger than those from the southern South China Sea (181-208 mm).

A character that was found to be useful in distinguishing specimens from the Indian Ocean was depth of the pterygoid notch, which showed only slight overlap with specimens from any of the other geographic areas - only 6.3% of specimens were in the area of overlap (Fig. 10). Adult-sized specimens with a notch depth of less than 11 mm can apparently be assumed to be from the Indian Ocean with high probability (Fig. 10).

Table 3. Skull morphometrics and meristics for adult-size *phocoenoides-* and *asiaorientalis*-type finless porpoises. The final column indicates level of significance of difference between means, using a t-test.

Measurement	*phocoenoides*-type			*asiaorientalis*-type			Signif.#
	Mean ± s.d.	Range	n	Mean ± s.d.	Range	n	
Condylobasal Length	211.4 ± 16.66	181-245	103	229.5 ± 10.33	209-251	64	***
Length of Rostrum	74.6 ± 7.62	62-92	103	86.8 ± 4.88	77-97	65	***
Width of Rostrum at Base	70.9 ± 5.42	60-84	107	68.6 ± 4.17	60-79	66	**
Width of Rostrum at 1/2 Length	55.8 ± 5.24	45-68	74	53.0 ± 3.55	44-60	64	***
Width of Rostrum at 3/4 Length	43.6 ± 4.43	34-53	69	42.7 ± 2.78	36-49	62	ns
Width of Premaxillae at 1/2 Length	29.3 ± 2.82	22-36	73	28.2 ± 2.85	22-34	60	*
Greatest Width of Premaxillae	39.1 ± 3.62	31-49	97	40.5 ± 2.53	36-46	66	**
Preorbital Width	117.7 ± 8.25	103-107	104	120.3 ± 6.89	106-137	65	*
Postorbital Width	137.0 ± 10.41	120-159	97	143.3 ± 6.14	131-156	59	***
Zygomatic Width	141.0 ± 11.42	120-166	91	149.2 ± 6.12	138-165	63	***
Parietal Width	117.4 ± 7.91	104-136	106	121.8 ± 5.62	111-137	66	***
Width of External Nares	29.2 ± 2.49	24-43	106	28.0 ± 1.65	24-31	66	***
Width of Internal Nares	42.3 ± 4.44	25-51	96	43.4 ± 2.80	37-52	65	ns
Length of Temporal Fossa	54.6 ± 5.77	43-67	98	56.6 ± 3.82	48-78	66	*
Height of Temporal Fossa	32.9 ± 3.76	24-42	101	34.8 ± 3.23	26-42	66	***
Length of Orbit	44.8 ± 4.31	36-54	103	43.8 ± 2.56	38-49	64	ns
Length of Antorbital Process	16.0 ± 2.78	9-22	99	20.2 ± 3.07	14-31	66	***
Length of Upper Toothrow	63.2 ± 5.87	57-76	102	71.2 ± 4.39	61-81	65	***
Length of Mandible	154.2 ± 11.03	126-176	62	164.5 ± 71.5	150-180	57	***
Height of Mandible	45.7 ± 4.30	36-54	61	50.1 ± 2.70	43-56	59	***
Length of Mandibular Symphysis	15.5 ± 2.31	10-20	62	16.4 ± 1.83	12-21	58	*
Depth of Pterygoid Notch	16.5 ± 5.11	3-30	60	18.8 ± 3.33	11-26	64	**
Greatest Upper Tooth Count	18.5 ± 1.27	15-22	102	18.4 ± 1.15	16-21	66	ns
Greatest Lower Tooth Count	18.9 ± 1.35	16-22	64	17.6 ± 1.23	15-20	59	***
Tooth Diameter (LL)	2.2 ± 0.32	1.7-3.0	16	2.4 ± 0.27	1.9-3.0	36	*

\# Level of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns not significant ($p > 0.05$).

DISCUSSION

Implications for Taxonomy

Information from the literature suggested that the two major geographic types of the finless porpoise can be distinguished based on the width of the dorsal ridge (<1.3 cm in the *asiaeorientalis*-type and >3.4 cm in the *phocaenoides*-type). At present, I know of no evidence for intermediate specimens from the area where the two types overlap in distribution (although some uncertainty exists for the Taiwan Strait and East China Sea), nor anywhere else throughout the range. In addition, most (ca. 92%) of the specimens can be distinguished based on a plot of length of rostrum vs. width of rostrum at base (see Fig. 7). Sympatric distributions with no interbreeding would clearly support the concept of two separate species. However, it should be cautioned that our knowledge of the finless porpoise from this area is incomplete. Sample sizes are still very small, and there is some uncertainty as to the exact collection locality of most of the specimens from the Taiwan Strait and East China Sea. In addition, the ambiguous positions of the two specimens of unknown type in the PCA and rostrum shape analyses do not provide support for this.
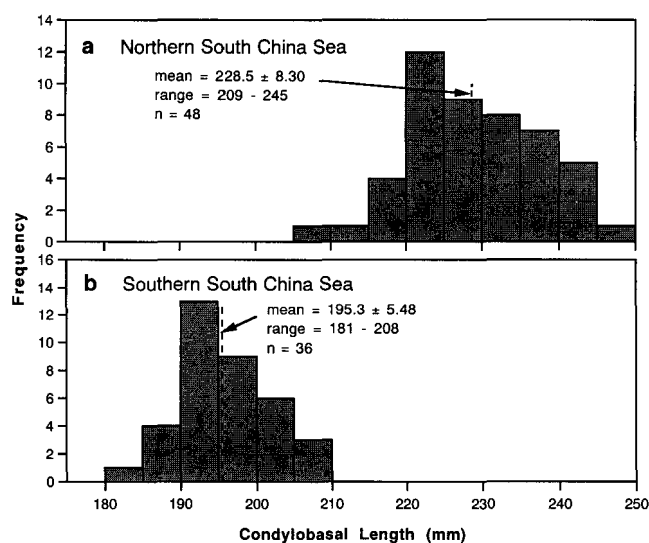

Fig. 9. Histogram of condylobasal length measurements for specimens from the northern (a) and southern South China seas (b).

As expected, there is evidence for several different geographical forms within each major type. The Yangtze River form is thought to be distinct due to habitat differences
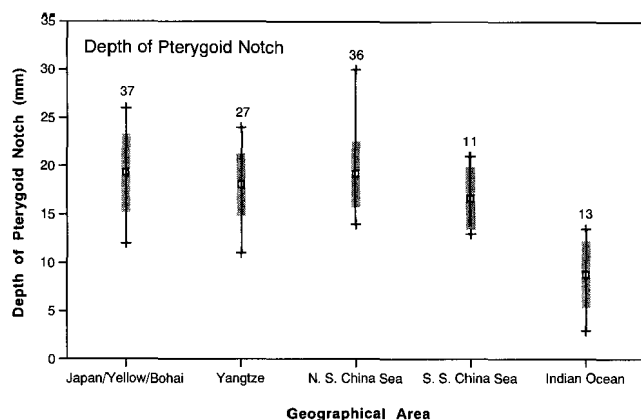
Fig. 10. Boxplot of depth of pterygoid notch among finless porpoises from different areas. Display same as in Fig. 5.

associated with a riverine existence, and also is darker in colour than those porpoises in coastal waters of northern China and Japan (Zhang, 1997). Because of the poor separation of Japanese and Yellow/Bohai seas specimens in the PCA, and the absence of any known characters that would reliably distinguish them, I do not find sufficient evidence to separate them at this point. Therefore, within the *asiaeorientalis*-type, it appears that there may be two well-distinguished forms: a Yangtze River form, and a Japan/Yellow/Bohai seas form.

Within the *phocaenoides*-type, northern and southern South China Sea specimens are clearly separable based on size alone, with apparently little or no overlap in the size of adult skulls. The Indian Ocean specimens overlapped with both other subspecies in the PCA, but I believe there is marginally-valid evidence to distinguish them as a separate form. This study has shown that the depth of pterygoid notch is much smaller in Indian Ocean specimens than those from other areas, apparently with almost no overlap. The scant literature on Indian Ocean finless porpoises also contains some suggestion of possible coloration differences (Pilleri & Gihr, 1972), and the Thai-Malay Peninsula and western islands of Indonesia appear to provide a possible dividing line. Therefore, I provisionally recognize three forms: a northern South China Sea form, a southern South China Sea form, and an Indian Ocean form.

Several of the proposed forms had been recognized as distinct in previous studies. However, the present study also found evidence for multiple stocks of finless porpoises in the South China Sea and Indian Ocean, which has not been indicated in the literature before. The main reason for this is probably that previous studies have not used adequate samples from within these areas to detect such differences. Most previous studies involving South China Sea animals used only specimens from the vicinity of the Taiwan Strait, at the very northern limit of the South China Sea. Indian Ocean specimens in previous studies have been mostly from Pakistan (Pilleri & Gihr, 1972, 1975). Amano et al. (1992)

did include a few specimens from Borneo and Singapore in their study, but the sample was small and some data were from literature reports.

The present analysis suggests that the differences between the northern and southern form finless porpoises in the South China Sea are mainly differences in the skull size of adults. At this time, it is impossible to determine if there are other differences between them as well (such as coloration, external morphological, postcranial, or genetic differences). The literature gives no indication that stocks from southern and northern parts of the South China Sea will likely be found to have any obvious external differences, other than size. However, the Yangtze River/northern China/Korea/Japan forms (currently classified as *N. p. asiaeorientalis* and *N. p. sunameri*) are known to be very different, with obvious external distinctions, such as differences in the colour pattern and the form of the dorsal ridge (Gao, 1991; Gao & Zhou, 1995a; Zhang, 1997). Other, more subtle, differences are also known (Amano et al., 1992; Kasuya, 1999). The main hindrance to a suitable taxonomic revision of the genus at this point appears to be the paucity of specimens and data available from very large portions of the range (e.g., the Persian Gulf area, the central Indian Ocean, and large portions of southeast Asia). Northern China and Japan, in contrast, have been relatively well represented. A study that resolves these remaining problems, and provides a more representative picture of the morphological variation present within the genus throughout its range, is thus still needed. I hope to update the current study, and to satisfy this shortcoming before it is finalized.

The affiliations of the narrow-ridge specimens collected from the East China Sea and Taiwan Strait areas are still controversial. In a sample of 21 finless porpoise specimens from Fujian Province in the Taiwan Strait area[1], 4 (19%) possessed narrow dorsal ridges, and the remainder had the wide dorsal ridge typical of South China Sea animals (Huang et al., 2000). Some authors have suggested that these narrow-ridge animals are members of the Yellow/Bohai seas population (Gao, 1991; Gao & Zhou, 1993, 1995a), while others have suggested that they are members of the Yangtze population (Wang, 1992a, b). The first suggestion is more plausible, as the Yangtze River animals are thought by most to be restricted to fresh water. It is also possible that they represent a yet-undescribed form of finless porpoise. Until a suitable series of specimens is examined and compared with specimens from adjacent areas, their identity will remain equivocal.

Genetic work in progress on specimens from throughout the range will greatly assist in efforts to resolve the taxonomy of this group. Preliminary molecular genetic work, using mtDNA analyses of specimens from Hong Kong, southern Fujian Province, Japan, and Korea, is currently in progress. Further work, with larger samples, and probably the inclusion

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1 Unfortunately, because the skulls of these specimens were not available for examination by the author in this study, these actual specimens are not represented in the present study. The specimens from this area that were available to me were either of unknown or wide dorsal ridge width.

of additional genetic markers, will be needed to shed additional light on the issue of higher-level taxonomy.

Implications for Conservation and Management

Regardless of the final determination on the taxonomic rank (species or subspecies) of the two major types, it is clear that these are distinct geographic types. Likewise, each of the proposed geographic forms would presumably represent a unique genetic entity, and therefore should be managed separately. It is possible that there are additional geographic forms to those shown in this paper, especially from the Indian Ocean and East China Sea, where available specimens of the species are at present sparse. It is also very likely that there are multiple reproductively-isolated populations or stocks within each of the forms. In fact, the latter has already been demonstrated for the Japanese (*sunameri*) form by Yoshida et al. (1995).

The finless porpoise's coastal habits make it highly vulnerable to impacts due to human activities such as incidental kills in fisheries, prey depletion, vessel collisions, and habitat loss and degradation. Therefore, research to further examine the population/stock structure of the finless porpoise throughout its range should be conducted as a matter of priority. This work would be most fruitful if it focussed on the use of molecular genetic techniques, which appear to be ideally suited to questions of population distinctness. In addition, large numbers of adequate samples for analysis can be collected in a short period of time with appropriate sampling programs. Such programs, which either sample specimens that die and strand, or sample carcasses taken incidentally in fisheries, should be set-up in as many portions of the range of the genus as is possible. A cooperative project will be needed to coordinate collection and processing of samples from widespread locations. This should be pursued despite the difficulties involved in such work.

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APPENDIX A: Review of *Neophocaena* Nomenclature.

Delphinus phocaenoides G. Cuvier, 1829
The type specimen was supposedly collected from the Cape of Good Hope (South Africa) by the French naturalist J. J. Dussumier in 1827. Although there has been a good deal of controversy about the locality of origin of the type specimen (see discussions in Hershkovitz, 1966; Robineau, 1990; Rice, 1998; Kasuya, 1999), it is now generally accepted that the specimen was actually collected along the Malabar coast of India. The type is preserved in the Museum National d'Histoire Naturelle, Paris (MNHN A3086 - Robineau, 1990), and it was examined by the author as part of this study. This is the senior synonym of the tropical form.

Delphinus melas Schlegel, 1841
This species was described based on a specimen from Japan, and the type is still in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH 23079) (see review of its history in van Bree, 1973). It was examined for this study. Schlegel's brief description was followed by a more detailed description in Schlegel (1844 - often erroneously cited as Temmink & Schlegel, 1844). Van Bree (1973) clarified that the name is preoccupied by *Delphinus melas* Traill, 1809, which is in the synonymy of *Globicephala melas* (long-finned pilot whale). Therefore, the name is a junior primary homonym, and therefore unavailable.

Delphinapterus molagan Owen, 1866
Owen (1866) described this species based on a drawing of a specimen from India. Apparently, no type specimen was collected. Based on the collection locality in India (an area within the exclusive range of the tropical form of finless porpoise), I consider the name to be a junior synonym of the tropical form.

Neomeris kurrachiensis Murray, 1884
The type specimen was collected from Kurrachee (Karachi, in present-day Pakistan) (Murray, 1884). There is apparently a finless porpoise skull in the Karachi Museum, which is presumably the type of this species. However, it does not appear to have been re-examined recently. Since the type was collected in Pakistan (within the exclusive range of the tropical form), the name probably represents a junior synonym of the tropical form. It should be examined to confirm its affinity.

Neomeris asiaeorientalis Pilleri & Gihr, 1972
Pilleri & Gihr (1972) described this species, based on a specimen from the Yangtze River in the collection of the Museum of Comparative Zoology, Harvard University (MCZ 19998). The type specimen was examined by the author. This is the senior synonym of the temperate form.

Neophocaena sunameri Pilleri & Gihr, 1975
This species name represents a renaming of *Delphinus melas* Schlegel, 1841, the species earlier described from Japanese waters, but later found to be preoccupied (see above). The holotype, a specimen in the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH 23079), was measured by the author. The name is a junior synonym of the temperate form.

Name Priority
From a review of the above, it is apparent that the valid name for the temperate form, if it is found to be a distinct species, would be *Neophocaena asiaeorientalis* (Pilleri & Gihr, 1972). *Neophocaena phocaenoides* (G. Cuvier, 1829) would thus be restricted to the tropical form.

APPENDIX B: Specimens Examined.

asiaeorientalis-type - BMNH 1902.6.10.65, 1922.6.26.1; LACM 86041; MCZ 19996-19997, 19998 (*asiaeorientalis* holotype), 2000; NJNU 8007, 8106, 8108, 8109, 8113-8118, 8202, 8204, 8205, 8218-8223, 8226, 8227, 8303-8305, 8407-8409, 8420, 8617-8619, 8621, 8907, 8913, 8916, 8918, 9009, 9031, 9034, 9035, 9111, 9112, 9117, 9119; NSMT no #, 1879, 23751, 24659, 24660, 24850, 24908, 24911, 24946, 24949, 24950, 24953, 24955-24957, 24963, 24964, 27855, 28371, 29891, 30114, 30132, 32428; RMNH 23079 (*sunameri* holotype); SMNS 45698; USNM 51907, 239990-240003, 240862, 241503, 550473; ZMA 17.942.

phocaenoides-type - BIMS no # (n = 3), 10; BMNH 1889.8.6.1, 1903.9.12.3, 1966.12.6.1; BNHS M 5968; CKU PT-97-01; CUMZ 003, 004; IM no #; LACM 54594; MEPA 13; MNHN A.3086 (*phocaenoides* holotype), A.3087; MSCU no #, 001, 003; NJNU 8720-8723, 9059, 9061, 9062, 9065-9067, 9069, 9084, 9085, 9127, 9184-9186; NMNS 732, 936, 1368, 1378, 3220; OPCF NP78-06/03, NP95-25/12, NP95-28/11, NP96-01/06, NP96-07/09, NP96-08/01, NP96-11/01, NP96-12/01, NP96-13/01, NP96-27/06, NP97-09/09, NP97-11/10, NP97-12/04, NP97-23/01, NP97-26/01, NP98-09/25, NP98-15/11, NP98-23/06, NP99-16/07, NP99-17/11, NP99-31/05, NP99-31/10; NTOU 20; PMBC 11645, 11648, 14629-A, 14629-B; RMNH 23566; SMNS 42496, 45679-45687, 45691, 45694-45697, 45699-45701; SMZ no # (n = 3), 71-18; SONG U no 3, 1942; TM no # (n = 2); UNIMAS NPHO-01; USNM 550489; WTCB 2; WTVL 1-3, 6; WTVT 1-4, 6-16, 18-24; ZMA 15.308, 20.292; ZRC no #, 4.1571A, 4.1571B.

Unknown type - NJNU 9068, 9130; USNM 49544, 504910.

APPENDIX C: Museum and Collection Acronyms.

BIMS, Bangsaen Institute of Marine Science, Chonburi, Thailand; BMNH, British Museum (Natural History), London, U.K.; BNHS, Bombay Natural History Society, Mumbai, India; CKU, Chen Kung University, Tainan, Taiwan; CUMZ, Natural History Museum, Chulalongkorn University, Bangkok, Thailand; IM, Indian Museum, Calcutta, India; LACM, Los Angeles County Museum of Natural History, CA; MCZ, Museum of Comparative Zoology, Cambridge University, Boston, MA; MEPA, Anthony Preen's personal collection, New South Wales, Australia; MNHN, Muséum national d'Histoire naturelle, Paris; MSCU, Department of Marine Science, Chulalongkorn University, Bangkok, Thailand; NJNU, Nanjing Normal University, Nanjing, China; NMNS, National Museum of Natural Science, Taichung, Taiwan; NSMT, National Science Museum, Tokyo; OPCF, Ocean Park Conservation Foundation, Hong Kong; PMBC, Phuket Marine Biological Center, Thailand; RMNH, Rijkmuseum van Natuurlijke Historie, Leiden, Netherlands; SONG U, Songkhla Unversity, Hat Yai, Thailand; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SMZ, Sarawak Museum, Kuching, Malaysia; SWFSC, Southwest Fisheries Science Center, Marine Mammal Synoptic Collection, La Jolla, CA; TM, Trivandrum Museum, Trivandrum, India; UNIMAS, Universiti Malaysia Sarawak, Kuching, East Malaysia; USNM, National Museum of Natural History, Washington, D.C.; WT CB, Cua Be Whale Temple, Nha Trang, Vietnam; WT VL, Vinh Loung Whale Temple, Nha Trang, Vietnam; WT VT, Vung Tau Whale Temple, Vung Tau, Vietnam; ZMA, Zoological Museum, University of Amsterdam, Netherlands; ZRC, Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore.