# Geographic Variation in Skull Morphology of Humpback Dolphins (*Sousa* spp.)

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## Abstract

The taxonomy and systematic relationships of humpback dolphins (genus *Sousa*) are highly confused. This is largely due to a lack of data and samples from large portions of the range of the genus, and confusing and seemingly contradictory patterns of variation in available external morphometric, skeletal morphometric, and molecular datasets. To help clarify the situation, we measured 222 skulls of humpback dolphins originating from throughout most regions of the range of *Sousa*. While patterns of cranial variation appeared to be relatively conservative, there was evidence for three groups: (1) Atlantic Ocean/ West Africa, (2) Western Indian Ocean, and (3) Eastern Indian Ocean/Pacific Ocean. These would appear to correspond to the *teuszii*, *plumbea*, and *chinensis* forms, respectively. No taxonomic revisions are recommended at this time, and the conservative view of two species (*S. teuszii* in West Africa and *S. chinensis* in the Indo-Pacific) can be defended for the time being as a pragmatic approach. The distinctness of *S. teuszii* is clearcut, but other taxonomic decisions should await further studies of molecular genetics and morphometrics, currently underway.

**Key Words:** cranial morphology, geographic variation, humpback dolphin, morphometrics, skull, *Sousa chinensis*, *Sousa plumbea*, *Sousa teuszii*, systematics, taxonomy

## Introduction

The taxonomy and systematics of the humpback dolphins (genus *Sousa*) have remained highly controversial, despite recent investigations of these animals in areas of their range not previously studied (see reviews in Jefferson & Karczmarski, 2001; Ross, 2002). Interestingly, the cytochrome b analysis by LeDuc (1997; LeDuc et al., 1999), which compared all but one of the delphinine dolphins, did not support the long-held relationship among *Sousa*, *Steno*, and *Sotalia*. Instead, *Sousa* grouped with a completely different set of genera (*Stenella*, *Delphinus*, *Tursiops*, and *Lagenodelphis*) in their phylogenetic tree. That study was highly preliminary, however, and further study will be necessary to determine the phylogenetic relationships among *Sousa*, *Steno*, and *Sotalia*.

More important for conservation, however, is the taxonomy below the genus level, and this also is controversial. Hershkovitz (1966) listed no fewer than 23 species names under the synonymies of those species now known to be in the genus *Sousa*, although some of these are clearly just name recombinations and alternate spellings. Over the years, nine distinct nominal species have been described (see review in Ross et al., 1994; Appendix III). The validity of most of these has been challenged, and some simply have been ignored because they were published in obscure references. Ross et al. (1994) and Ross (2002) accepted three of the five species they reviewed as valid, but most other recent authors considered only *S. chinensis* and *S. teuszii* to be distinct species. Even this conservative view has been challenged, however, and Cockcroft et al. (1997) suggested that all humpback dolphins are members of a single, highly variable species. Rice (1998), in his exhaustive review of marine mammal species, considered *S. chinensis*, *S. plumbea*, and *S. teuszii* to be valid, but gave no convincing arguments. In this scenario, *S. chinensis* occurs in the eastern Indian Ocean and Pacific, has light adult coloration, often with black spotting, and lacks the prominent dorsal hump; *S. plumbea* occurs in the western Indian Ocean, has dark grey adult coloration with little spotting, and a prominent hump; and *S. teuszii* occurs off West Africa and has a similar external appearance to that of *S. plumbea*

(see Ross et al., 1994, 1995; Van Waerebeek et al., 2004).

Recently, Ross et al. (1995) completed a preliminary study that demonstrated substantial variation in both the external and skeletal morphology of humpback dolphins, and Cockcroft et al. (1997) similarly showed variation in molecular structure, using mtDNA analyses. Both studies suffered from a paucity of specimens from certain parts of the range (especially Southeast Asia), and the patterns of variation among the different datasets did not agree (and in some cases, showed apparent contradictions). They were not able to resolve the taxonomy of this genus, and it became clear that further studies of morphological and genetic variation, with more representative samples, were needed to gain a clearer picture. We present this analysis of cranial variation and review of the taxonomic literature regarding *Sousa* as a contribution toward resolving the taxonomy of the genus, in conjunction with molecular genetic studies currently underway (see Rosenbaum et al., 2002).

## Materials and Methods

We measured a total of 222 skulls of humpback dolphins from throughout the range of the genus *Sousa* (Figure 1). A list of specimens used in the study is given in Appendix I, and a summary by geographic region is shown in Table 1. Each skull was assigned to a putative geographic form (*teuszii*, *plumbea*, or *chinensis*), based on its geographic origin and information in the literature (Table 1). West African specimens were assigned to the *teuszii* form, western Indian Ocean specimens (India to South Africa) to *plumbea*, and eastern Indian Ocean/Pacific specimens (east of India) to *chinensis*. Although we did not have data on external morphology and coloration for all specimens, when such data were available they supported the identifications.

Standard measurements (a subset of those from Perrin, 1975, with some minor modifications) were taken on each skull, using vernier calipers and dial calipers (Table 2). Measurements of greater than 10 mm were taken to the nearest millimeter; those of less than 10 mm to the nearest
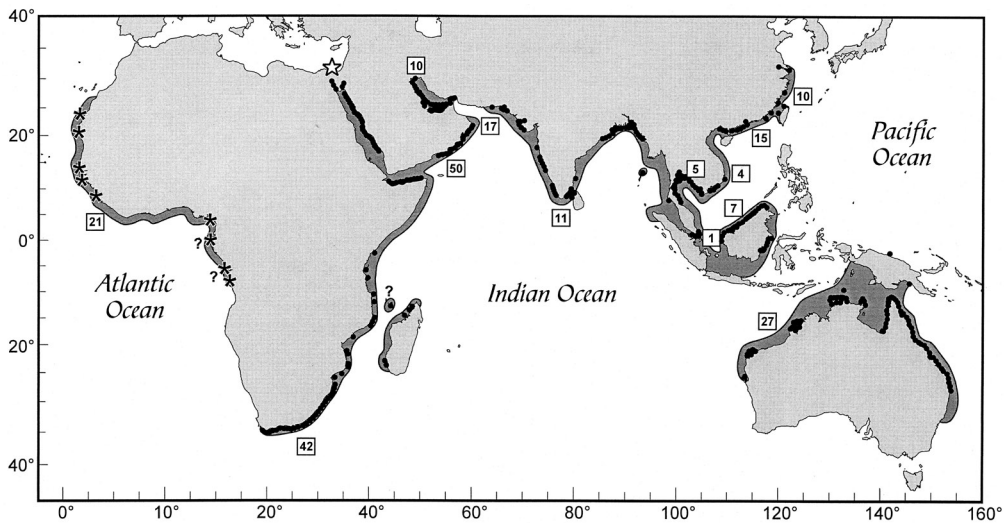


**Figure 1.** Map of the Indo-Pacific and Eastern Atlantic Oceans, showing the range of humpback dolphins and the number of skulls (numbers in boxes) examined from different areas in this study. The map shows locations of confirmed records (asterisks and black dots) modified from the International Whaling Commission (2003) and an extralimital record in the Mediterranean (star), as well as the presumed range (shading), based on known distribution and suitable habitat; ? = questionable sighting. Although shown here as a series of more-or-less continuous bands, the present occurrence of humpback dolphins throughout much of their range (e.g., West Africa [Van Waerebeek et al., 2004]; China [Jefferson, 2000]) is likely to be discontinuous. The hiatus in the Gulf of Oman is considered to be real and is supported by survey work (Baldwin et al., 2004).

**Table 1.** Summary of the humpback dolphin skull sample measured for this study

| Putative population | Geographic area | Form* | No. skulls | Total |
|---|---|---|---|---|
| West Africa | Mauritania | *teuszii* | 9 | 21 |
| | Senegal | *teuszii* | 10 | |
| | Cameroon | *teuszii* | 1 | |
| | Gabon | *teuszii* | 1 | |
| South Africa | South Africa | *plumbea* | 42 | 42 |
| Red Sea/ Arabian Peninsula | Red Sea/ Oman | *plumbea* *plumbea* | 7 43 | 50 |
| Persian Gulf | Persian Gulf | *plumbea* | 10 | 10 |
| Pakistan | Pakistan | *plumbea* | 17 | 17 |
| India | India | *plumbea*# | 11 | 11 |
| Southeast Asia | Borneo | *chinensis* | 7 | 17 |
| | Singapore | *chinensis* | 1 | |
| | Thailand | *chinensis* | 5 | |
| | Vietnam | *chinensis* | 4 | |
| China | Mainland China | *chinensis* | 10 | 25 |
| | Hong Kong | *chinensis* | 15 | |
| Australia | Australia | *chinensis* | 27 | 27 |
| Unknown | Unknown | unknown | 2 | 2 |
| | | | Total | 222 |

*Information in the literature on the extent of variation among these putative forms is at present incomplete, and, therefore, our classification here should be considered somewhat tentative.

#While there is evidence that both the *plumbea* and *chinensis* forms of the humpback dolphin occur in India (see Sutaria & Jefferson, 2004), there was little external morphological data available to assign skulls to specific forms. Most of the skulls came from the west coast of India, where apparently only the *plumbea* form occurs.

**Table 2.** List of measurements and meristics taken on humpback dolphin skulls

| Character | Variable no. in Perrin (1975) | Abbreviation |
|---|---|---|
| Condylobasal length | 1 | CBL |
| Length of rostrum | 2 | LRO |
| Width of rostrum at base | 3 | WRB |
| Width of rostrum at ½ length | 5 | WRH |
| Width of rostrum at ¾ length | 7 | WRT |
| Width of premaxillae at ½ 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 | GWIN |
| 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 |
| Greatest upper tooth count | 33/34 | UTC |
| Greatest lower tooth count | 35/36 | LTC |
| Tooth diameter (middle lower left)# | – | TD |

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

0.1 mm. We followed Amaha (1994) and used the higher tooth count between right and left sides; therefore, each specimen was given a single upper and a single lower tooth count. Because most of the specimens were beach-cast or museum acquisitions (many of them very old) and not collected as part of a dedicated research program, sex and total body length were unknown for many of the specimens; therefore, sexual dimorphism could not be studied. There were no indications of any bias in sex composition of the available sample, however, and we, therefore, believe that this should not affect the results. Preliminary presentations and analyses of portions of this dataset were given previously in Van Waerebeek et al. (2002) and Jefferson (2002a).

All measurements were taken by one of the authors (82% by TAJ).[1] To ensure that there was no significant bias associated with inter-observer

differences in how skull measurements were taken, we conducted an intercalibration exercise. Both authors independently measured the same ten skulls of long-beaked common dolphins (*Delphinus capensis*) at two different institutions (the USNM and ZMA), and compared the means of the resulting measurements using *t*-tests. We used multiple *t*-tests, rather than a multivariate MANOVA, because we were interested specifically in identifying which individual measurements showed differences between the way the two authors measured them. This often results from a slightly different spatial interpretation of

[1] Except for four skulls from Mauritania, which were measured by A. Samba-Ould-Bilal, a biologist of the Institut National de Recherche Océanographique et des Peches, Nouadhibou, Mauritania, who received practical training in craniometrics methodology from one of us (KVW).
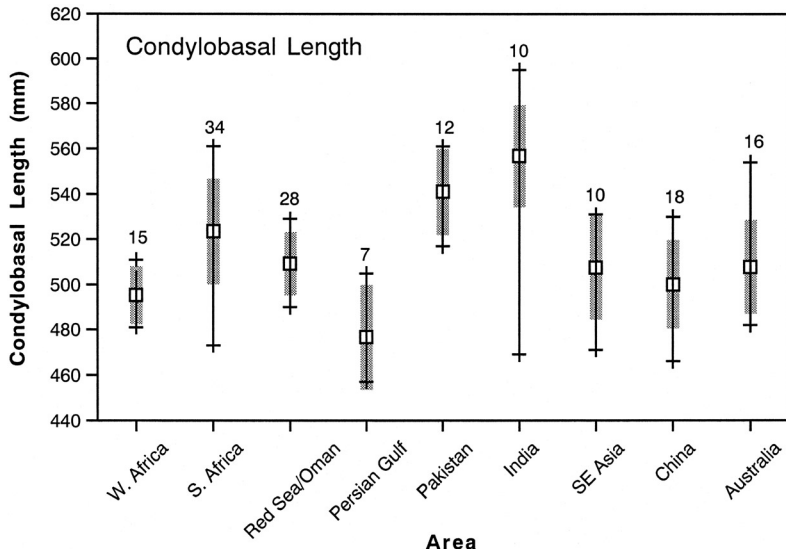
**Figure 2.** Geographic variation in the condylobasal length of humpback dolphin skulls. Squares are means, shaded boxes are ±1 standard deviation, vertical lines are ranges, and numbers are sample sizes.
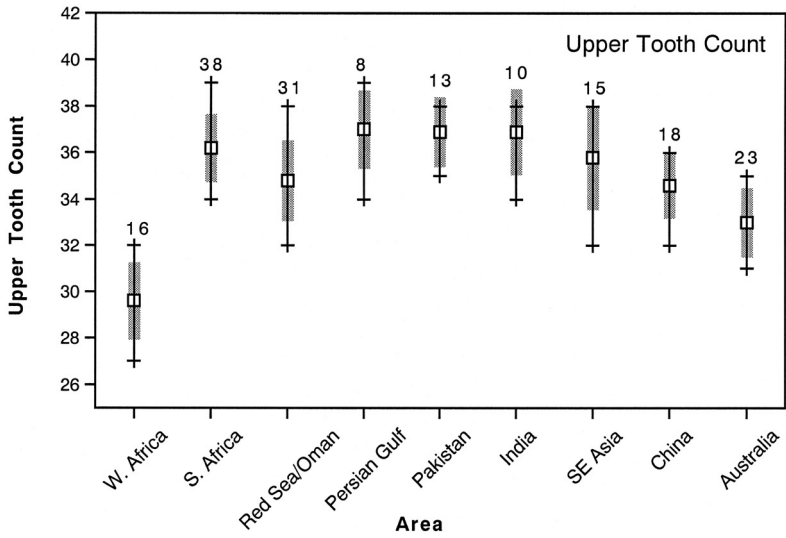


**Figure 3.** Geographic variation in the upper tooth count of humpback dolphin skulls. Squares are means, shaded boxes are ±1 standard deviation, vertical lines are ranges, and numbers are sample sizes.

**Table 3.** Factor loadings (unrotated solution) for the first three principal components; analysis was done on a matrix of correlation values, with all settings at default.

| Character | PC1 | PC2 | PC3 |
|---|---|---|---|
| Upper tooth count | -0.044138 | -0.783883 | 0.056403 |
| Condylobasal length | 0.733824 | -0.581257 | -0.123582 |
| Length of rostrum | 0.625392 | -0.688129 | -0.097233 |
| Width of rostrum at base | 0.878666 | 0.257898 | -0.007112 |
| Width of rostrum at ½ length | 0.673651 | 0.428640 | -0.070413 |
| Width of premaxillae at ½ length | 0.654866 | 0.345131 | -0.246471 |
| Greatest width of premaxillae | 0.743098 | 0.189691 | -0.109145 |
| Preorbital width | 0.889186 | 0.181018 | -0.083884 |
| Postorbital width | 0.943653 | 0.064432 | -0.118129 |
| Zygomatic width | 0.932221 | 0.119673 | 0.042230 |
| Parietal width | 0.456697 | 0.157149 | -0.599614 |
| Width of external nares | 0.499540 | -0.024744 | 0.459998 |
| Width of internal nares | 0.584091 | 0.107568 | 0.648638 |
| Length of temporal fossa | 0.751385 | -0.069916 | 0.365231 |
| Height of temporal fossa | 0.522462 | -0.051465 | 0.647318 |
| Length of orbit | 0.563191 | -0.285968 | -0.178760 |
| Length of antiorbital process | 0.493338 | -0.102152 | -0.462691 |
| Length of upper toothrow | 0.384261 | -0.622791 | -0.090385 |
| Variance explained | 0.451332 | 0.134595 | 0.106640 |
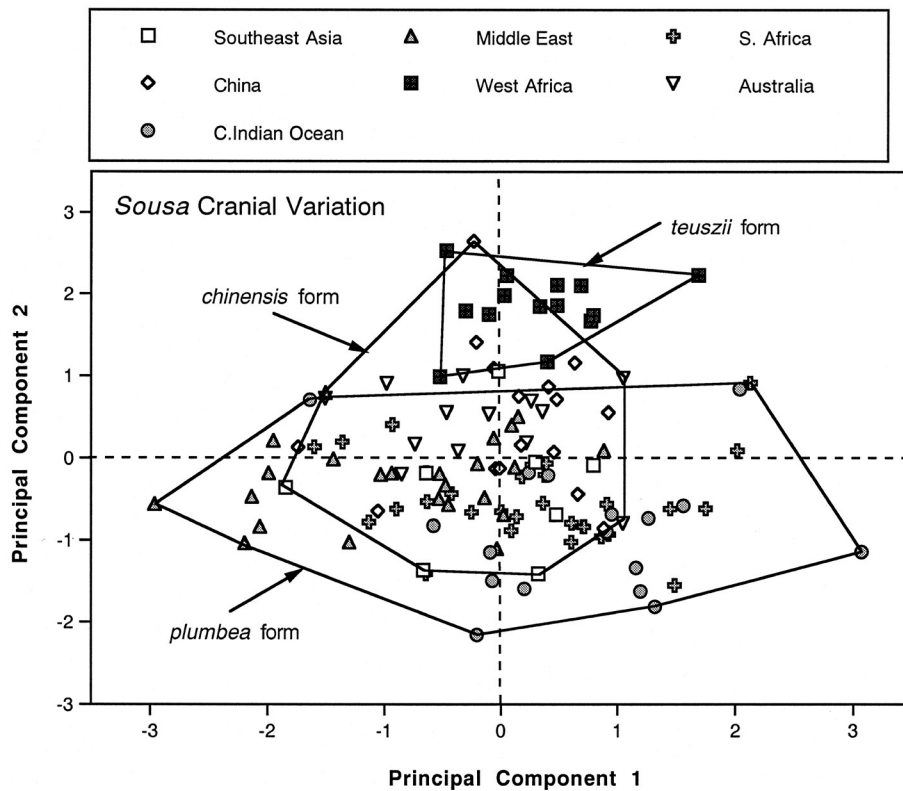


**Figure 4.** Plot of the first two principal component scores for humpback dolphin skulls from different geographic regions
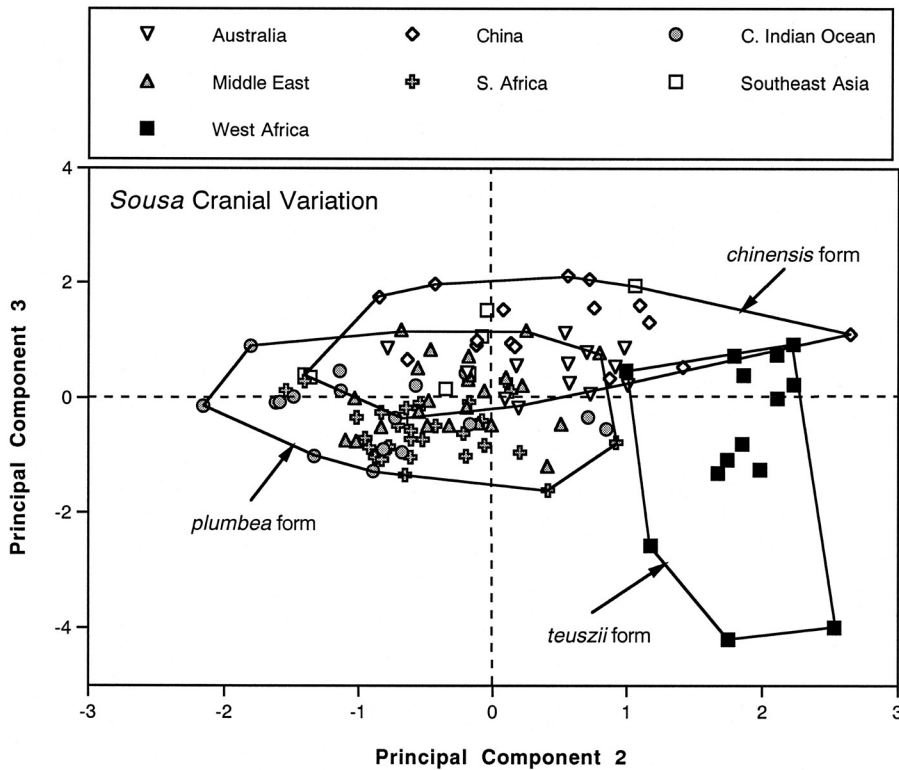
**Figure 5.** Plot of the second and third principal component scores for humpback dolphin skulls from different geographic regions; notice the strong separation of West African specimens.

cranial reference points. We were not interested in examining interactions among the variables here. Only one measurement, length of orbit, exhibited significant differences between the two observers ($p<0.05$). This measurement was subsequently deleted from analyses (see Jefferson & Van Waerebeek, 2002).

We were faced with a difficulty in determining which of the skulls to include in the adult series for the analyses. Although none of the skulls examined had fully fused cranial bones (in fact, most showed no fusion to speak of in key sutures, e.g., maxillary-premaxillary, frontal-occipital, pterygoid-basioccipital, pterygoid-palatine sutures), many skulls were quite large and heavily ossified, indicative of maturity. Most skulls of dolphins of the genus *Sousa* do not appear to attain fusion of the maxillary-premaxillary suture, as they do in other delphinid genera, for instance, *Delphinus*, *Stenella*, and *Lagenorhynchus* (see Perrin & Heyning, 1993; Van Waerebeek, 1993). In general, *Sousa* skulls seem to develop cranial fusion at a late developmental stage (if at all) and, consequently, cranial sutures of beach-cast skulls (even from adult animals) may disarticulate secondarily through

beach-wear. In addition, the great geographic variation in mean condylobasal length (CBL) precluded us from using a minimum CBL cut-off for selecting adult skulls.

We had no choice, therefore, but to use subjective criteria to judge skulls as "adult" for the analyses, including relative degree of ossification and fusion of cranial bones, development of rostral bones relative to the neurocranium, overall massiveness of skull, inter-bone motility (under manual pressure), and degree of closure of tooth pulp cavity. This suite of characters is based on our experience with this and other species of small odontocetes (see Jefferson, 1996; Jefferson, 2002b; Jefferson & Van Waerebeek, 2002; Reyes & Van Waerebeek, 1995; Van Waerebeek, 1993; Van Waerebeek et al., 1990). After evaluation, we considered 158 skulls with a CBL range of 457-595 mm to be adult, 50 skulls with a range of 274-536 mm were judged to be subadult, and a further 14 with a range from 470-535 mm were of indeterminate developmental stage. Only skulls in the first category, and those known to be from sexually mature specimens, were included in adult-series analyses. The only exception was for
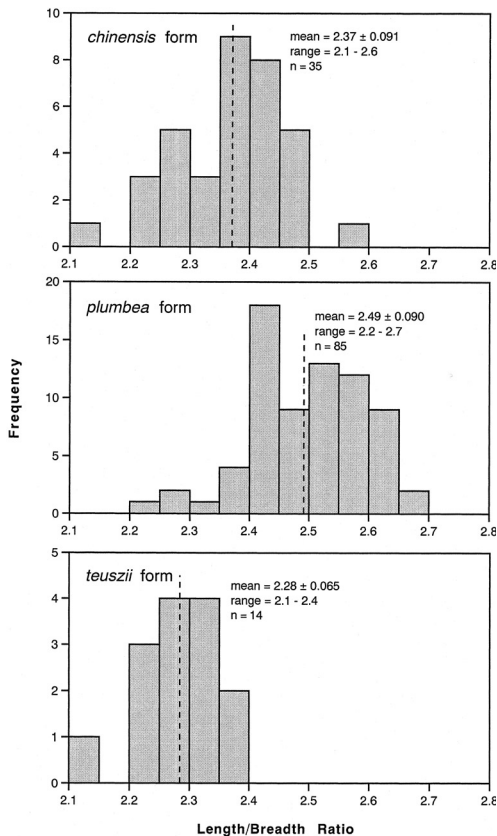
**Figure 6.** Histograms of condylobasal length/zygomatic width ratios of adult skulls of the three different forms of humpback dolphins; dashed line indicates mean.



**Figure 7.** Representative skulls of humpback dolphins from different regions of the range: *chinensis*-form skull from Hong Kong (OPCF SC97-31/05-B—top); *plumbea*-form skull from the Persian Gulf (BMNH 70.1506—middle); and holotype of *S. teuszii* from West Africa (BMNH 1893.8.11—bottom); notice the shorter, wider rostrum of the West African specimen.

tooth counts, in which all specimens with accurate tooth counts were used. Despite our best efforts, we have almost certainly inadvertently accepted a few skulls from subadult specimens; however, we have no reason to believe that this shortcoming showed bias with geographic location and, therefore, it should not significantly affect the results of this study.

A principal components analysis (PCA) was performed using *STATISTICA*™ V4.1 (Statsoft, Inc.). Because multivariate analyses are sensitive to missing data, measurements were excluded if data were missing from more than four specimens. For the remaining measurements with incomplete data, missing values were estimated using the mean substitution method available in *STATISTICA*™ (which calculates a mean for that variable from the overall dataset, not just from that group). The PCA was performed on the remaining dataset (n=123 skulls), which was composed of 17 morphometric and one meristic
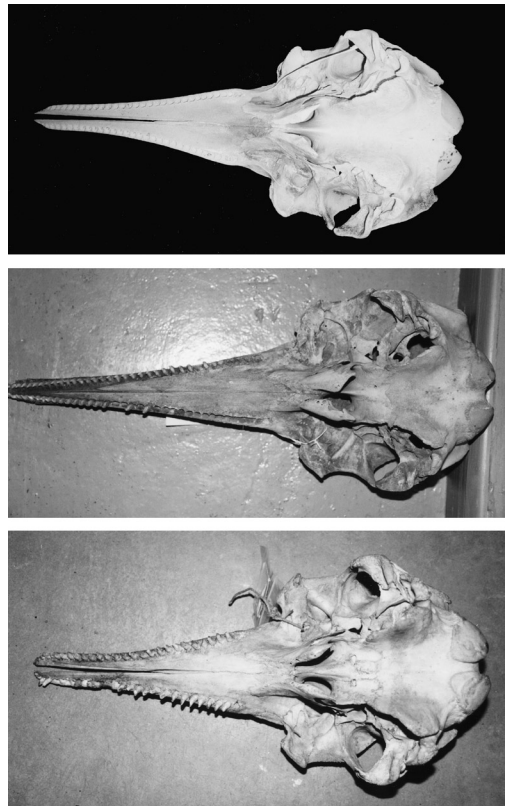
character (greatest upper tooth count). Various rotating solutions were attempted (unrotated, varimax, and quartimax), and the solution that provided the best separation was used.

### Results

There was a great deal of geographic variation in the CBL of humpback dolphin skulls from throughout their range (Figure 2). Differences among specimens from separate areas were highly statistically significant (one-way ANOVA, F=10.600, df=8, $p<0.001$); however, few clearcut patterns related to geography were evident, and Tukey's pairwise tests showed significant differences for several comparisons ($p<0.05$). West African (*teuszii* form) and Persian Gulf humpback dolphins had the shortest skulls.

**Table 4.** Summary of cranial morphometrics and meristics for three forms of *Sousa*, based on adult specimens

| Measurement | *teuszii* form | | | | *plumbea* form | | | | *chinensis* form | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Range | n | Mean | SD | Range | n | Mean | SD | Range | n |
| Upper tooth count | 29.6 | 1.49 | 27-32 | 14 | 36.5 | 1.46 | 33-39 | 79 | 34.6 | 2.01 | 31-38 | 40 |
| Lower tooth count | 28.7 | 1.03 | 28-31 | 7 | 34.5 | 1.21 | 32-37 | 63 | 33.0 | 1.79 | 29-38 | 42 |
| Tooth diameter | 6.70 | 0.574 | 5.8-7.4 | 8 | 5.99 | 0.469 | 4.8-6.9 | 54 | 6.31 | 0.522 | 5.4-7.3 | 27 |
| Condylobasal length | 495.4 | 10.46 | 481-511 | 14 | 520.9 | 26.96 | 457-595 | 80 | 502.3 | 24.56 | 405-554 | 38 |
| Length of rostrum | 294.9 | 8.15 | 279-308 | 14 | 322.2 | 20.22 | 276-377 | 81 | 309.0 | 16.05 | 277-350 | 37 |
| Width of rostrum at base | 114.5 | 4.94 | 107-127 | 15 | 107.5 | 8.04 | 90-131 | 82 | 109.3 | 5.28 | 96-118 | 47 |
| Width of rostrum at ½ length | 48.9 | 2.77 | 44-54 | 14 | 46.0 | 3.17 | 37-55 | 78 | 46.1 | 2.79 | 40-53 | 39 |
| Width of rostrum at ¾ length | 34.1 | 3.01 | 28-38 | 15 | 32.7 | 2.84 | 27-41 | 78 | 32.0 | 2.33 | 28-38 | 37 |
| Width of premaxillae at ½ length | 33.6 | 3.91 | 27-44 | 15 | 29.3 | 3.31 | 21-39 | 78 | 29.6 | 3.08 | 23-37 | 39 |
| Greatest width of premaxillae | 85.9 | 2.40 | 83-90 | 15 | 80.8 | 5.32 | 70-93 | 85 | 80.4 | 4.45 | 72-91 | 45 |
| Preorbital width | 199.1 | 5.03 | 192-210 | 15 | 186.4 | 12.4 | 159-219 | 79 | 188.5 | 8.35 | 169-200 | 45 |
| Postorbital width | 223.6 | 24.59 | 209-312 | 16 | 210.7 | 14.26 | 176-244 | 77 | 212.0 | 8.42 | 192-226 | 45 |
| Zygomatic width | 217.1 | 6.86 | 209-239 | 16 | 207.8 | 14.48 | 177-243 | 85 | 212.60 | 9.08 | 192-230 | 45 |
| Parietal width | 162.7 | 15.14 | 142-183 | 15 | 154.4 | 8.56 | 133-175 | 85 | 145.3 | 5.34 | 136-155 | 43 |
| Width of external nares | 53.5 | 4.47 | 44-60 | 15 | 53.0 | 2.99 | 46-60 | 85 | 53.4 | 3.39 | 48-63 | 45 |
| Width of internal nares | 61.1 | 7.02 | 46-72 | 15 | 60.4 | 3.92 | 52-70 | 80 | 63.8 | 5.37 | 53-74 | 45 |
| Length of temporal fossa | 104.7 | 3.57 | 97-111 | 16 | 105.3 | 7.68 | 84-125 | 82 | 110.5 | 4.99 | 100-121 | 45 |
| Height of temporal fossa | 81.4 | 12.54 | 53-98 | 16 | 83.2 | 6.48 | 66-98 | 84 | 88.2 | 5.43 | 75-99 | 45 |
| Length of orbit | 55.5 | 2.42 | 51-59 | 15 | 56.8 | 3.20 | 49-65 | 81 | 56.2 | 2.33 | 51-63 | 45 |
| Length of antiorbital process | 43.1 | 3.17 | 39-49 | 14 | 42.1 | 4.53 | 32-51 | 82 | 39.4 | 2.87 | 34-47 | 45 |
| Length of upper toothrow | 255.9 | 8.05 | 242-270 | 14 | 281.1 | 17.58 | 238-323 | 76 | 272.4 | 14.58 | 246-309 | 39 |
| Length of mandible | 385.3 | 61.60 | 241-431 | 8 | 446.0 | 24.37 | 362-485 | 54 | 424.7 | 39.23 | 242-491 | 41 |
| Length of mandibular symphysis | 102.7 | 9.91 | 92-120 | 6 | 129.2 | 13.28 | 95-150 | 52 | 124.5 | 12.17 | 92-155 | 40 |
| Length/breadth ratio | 2.28 | 0.065 | 2.1-2.4 | 14 | 2.49 | 0.090 | 2.2-2.7 | 85 | 2.37 | 0.091 | 2.1-2.6 | 35 |

In contrast to the situation with skull length described above, tooth counts appeared to be relatively conservative (Figure 3). The only obvious exception was for West African specimens, which had very low upper tooth counts, an average of less than 30, as opposed to averages between about 33 and 37 for the Indo-Pacific specimens. Overall, differences among areas were highly statistically significant (ANOVA, F=54.883, df=8, $p<0.001$), and this is largely due to very low tooth counts in West African specimens (Tukey's pairwise comparisons with all other areas, $p<0.001$). The general pattern in the Indo-Pacific specimens was for a slightly decreasing average tooth count in the specimens from the far eastern part of the range (Southeast Asia, China, and Australia).

The PCA (unrotated solution) resulted in the calculation of three principal components (Table 3). PC1 explained 45.1%; PC2, 13.5%; and PC3, 10.7% of the overall variation. The PCA did not show complete separation of specimens from any geographic area, and the polygons for each area overlapped with at least one other region of the range (Figures 4 & 5).

There was not much separation on the PC1 axis (Figure 4), which generally reflects absolute size. Specimens from the western Indian Ocean (*plumbea* form, with a prominent dorsal hump) generally had lower scores on PC2 than those from the eastern Indian Ocean/Pacific (*chinensis* form, without a prominent hump). When separate polygons were drawn around these two putative forms, there was some evidence of separation (although the polygons still showed a great deal of overlap). Surprisingly, specimens from West Africa (which have a prominent hump) did not overlap those from the western Indian Ocean (also with a hump), but showed strong overlap with those from the eastern Indian Ocean/Pacific (not exhibiting a hump).

Plotting PC2 versus PC3 showed much better separation of the clusters for the three putative forms (Figure 5). Specimens from West Africa (*teuszii* form) showed a smaller area of overlap with the *chinensis* form and again complete separation from the *plumbea* form.

We computed the length/breadth ratio of the skull as the CBL divided by the zygomatic width. When comparisons were made among the three forms of humpback dolphins, the differences were significant (ANOVA, F=4.528, df=2, $p<0.05$), although none of the Tukey's pairwise comparisons was significant ($p>0.05$). It was clear that the *plumbea*-form specimens possessed relatively long and narrow skulls (Figures 6 & 7). Those of the other two types were relatively wider (lower length/breadth ratio), and the *teuszii*-form specimens had the lowest ratios. Skulls of

*chinensis*-form specimens were in between these two extremes. Summary statistics for measurements and meristics of the three forms are presented in Table 4.

## Discussion

This preliminary analysis of geographic variation in skull morphology of humpback dolphins has not provided a clearcut indication of the exact taxonomic relationships within the genus. For instance, in at least one area with high water temperatures (i.e., the Persian Gulf), humpback dolphins had small skulls, as expected; however, in other nearby areas with similarly high water temperatures (e.g., India and Pakistan), the skulls appeared to be much larger (see Figure 2). The major patterns of geographic variation evident in external morphology (see Ross, 1984; Ross et al., 1994, 1995) are not strongly reflected by our PCA results from cranial morphology. In particular, the two main geographic forms that are apparent from external features (i.e., those with and without a prominent dorsal hump) do not separate out strongly in some of the present results. Despite their closer geographical proximity and similar external morphology, the PCA results suggest that the West African and western Indian Ocean forms may not be closely related. The presence of the hump may be an example of convergent evolution, or an ancestral characteristic (plesiomorph) in *Sousa* and, thus, not particularly phylogenetically informative. As pointed out by earlier studies (e.g., Lal Mohan, 1985), it seems that craniological variation in the genus in general has been rather conservative. In other words, with the exception of the West African form, there do not seem to be dramatic differences in the skulls of humpback dolphins from different parts of the Indo-Pacific (even though these animals show strong variation in external morphology and coloration).

We did find support for the recognition of three types of humpback dolphins, however, based on the PCA results and differences in the length/breadth ratio of the skull. Specimens from the western Indian Ocean (*plumbea* form) have relatively long, narrow skulls (Figure 7). The relatively narrower skulls of the *plumbea* form are not simply a result of evolutionary lengthening of the skull, for while some *plumbea*-form populations (e.g., India and Pakistan) had very long skulls, others (e.g., Persian Gulf) showed very short skulls. In fact, they were the shortest of any represented in this study.

Although Ross (1984) doubted the species-level distinctness of the West African *S. teuszii*, several other studies have supported its validity, although

based on small or poorly interpreted samples (e.g., Pilleri & Gihr, 1972; Zhou et al., 1980). The present study did find convincing evidence of the distinctness of the West African (Atlantic) humpback dolphin, and there seems to be no doubt that this form represents a distinct taxonomic entity, in our opinion, at the species level. It has a relatively wide skull, with a shorter rostrum and much lower average tooth counts than other humpback dolphins. Its pronounced geographic isolation by a long stretch of cool-water habitat on the southwest coast of Africa probably existed for a long time, and this further supports its specific status.

In light of currently available information from both external morphometric (including coloration) and skeletal morphometric data (this study; Ross et al., 1995), it seems appropriate to recognize three geographic forms of humpback dolphin, without necessarily assigning a definitive taxonomic status to them at this point in time (see Figure 7 for views of representative skulls):

1. *Atlantic Ocean (West Africa):* These animals have a prominent dorsal hump, uniform grey adult coloration (except for a whitish belly and some dark spotting on the tail stock in some individuals), low tooth counts, very wide skulls, and short rostra. They correspond to the *teuszii* form, and their distribution appears to be limited to the coast of West Africa, from Morocco to Angola, with a large distributional gap on the southwest coast of Africa (Cape Town to southern Angola) between them and the *plumbea* form (Van Waerebeek et al., 2004).

2. *Western Indian Ocean:* Specimens of this form have a prominent dorsal hump, relatively uniform gray adult coloration, higher tooth counts, narrow skulls, and longer rostra. This is the *plumbea* form, which extends from South Africa to at least the Bay of Bengal (Rice, 1998). Recent surveys in the Andaman Sea areas of Langkawi Island, Malaysia, and Phuket Island, Thailand suggest that the distribution of the *plumbea* form may extend east to this area (L. Rajamani, Borneo Marine Research Unit; Kota Kinabalu, Malaysia; and S. Chantrapornsyl, Phuket Marine Biological Center, Phuket, Thailand, pers. comm.). Animals off the coast of Madagascar (Razafindrakoto et al., 2004; Robineau & Rose, 1984) presumably are of this type as well.

3. *Eastern Indian Ocean/Western Pacific Ocean:* These dolphins have no prominent dorsal hump, light gray to white adult coloration (often with prominent spotting), high tooth counts, relatively wide skulls, and relatively long rostra. This is the *chinensis* form, and the distribution extends from at least the Gulf of Thailand east to central China and northern Australia.

The Atlantic humpback dolphin apparently is isolated from other humpback dolphins by a distributional gap of at least 2,000 km on the southwest coast of Africa, which is dominated by cold upwelling associated with the Benguela Current System (see Jefferson & Karczmarski, 2001; Ross et al., 1994; Van Waerebeek et al., 2004). Although its precise southern range limit is not known, there are no confirmed records of *Sousa* along the stretch of coast between South Africa's False Bay and southern Angola. In addition, the Atlantic humpback dolphin has several distinct characteristics (described above) that would serve to separate it from the Indo-Pacific forms. Therefore, we strongly suggest that *S. teuszii* continue to be listed as a separate species.

Interestingly, there is some evidence to suggest that the *plumbea* and *chinensis* forms may overlap in distribution in the Bay of Bengal and perhaps the Andaman Sea. Specimens fitting the description of the *plumbea* form have been seen in the Andaman Sea (see above; Leatherwood & Clarke, 1983), and recently there have been sightings of animals very similar to the *chinensis* form from Southeast Asia along the coast of Orissa, eastern India (Sutaria & Jefferson, 2004). If these two forms are indeed found to be sympatric, and there is no evidence of interbreeding and hybridization/intergradation, then this would be compelling evidence for their specific distinctness. This is unconfirmed at this point, but is worthy of further investigation.

We must keep in mind, however, that the available data from the eastern Indian Ocean and western Southeast Asia are very fragmented at the moment. Due to the current lack of evidence for matching diagnostic characters in both external and skeletal morphometric characters, as well as conflicting genetic information (Cockcroft et al., 1997), it would be prudent not to list the two Indo-Pacific forms as separate species at this time. It would seem more appropriate to conservatively continue to designate them under *S. chinensis* until further studies can be done to shed light on their true status. Based on the results of the present study and those of Cockcroft et al. (1997), they are probably distinct at least at the subspecific level. No taxonomic revisions are suggested at this time, however.

Additional studies, especially molecular analyses examining multiple genetic markers, clearly are needed. The currently available studies of molecular genetic variation have largely been limited by sample size considerations or have been restricted to samples from specific portions of the range of the genus (Cockcroft et al. (1997); Porter, 1998; Smith-Goodwin, 1997). The only completed study that included samples from

throughout a significant portion of the range of the genus yielded somewhat confusing results (Cockcroft et al., 1997). It is appropriate to await the results of additional molecular genetic studies (currently underway by H. Rosenbaum and colleagues, including the senior author; see Rosenbaum et al., 2002), as well as further morphometric studies by G. J. B. Ross and colleagues (see Ross et al., 1995).

Despite the remaining uncertainty, one thing is clear. *Sousa* is a highly variable genus, and there eventually will be several geographic forms (and probably more than two species) recognized in this genus. It may take some time to fully settle the taxonomic controversies of this genus; however, in terms of conservation and management in the interim, it is important to treat each geographic form as an evolutionarily significant unit (ESU) and, therefore, representing one or more separate stocks for management, regardless of its final taxonomic rank.

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## Appendix I

*Specimens Examined* (Museum and institution acronyms are listed in Appendix II.): AM M12691; AMNH 120268; BIMS 003; BMNH 1866.2.5.2, 1882.1.2.1, 1893.8.1.1, 1901.2.16.1, 1903.9.12.2, 1914.1.14.1, 1924.9.11.1, 1937.6.22.1, 1948.3.13.1, 1948.3.13.2, 1954.9.9.5, 1962.7.19.1, 1965.1.6.3, 1984.1758, 1984.1759, 1984.1761, 1992.138, 1992.92, 70.1505, 1992.92, 70.1506, 1992.92, 70.1507, 70.1509, 70.1510, 73.1748; BNHS M 5965, M 5966, UN-45; CEPEC KVW-4030-OM; FMNH 99607; IFAN 114, 115, 116, 117, 118, 93-4; JCU NO#A, NO#B; LACM 72168; LFMRI BH8201, BH8801, GZ9101; MNHN 1897.654, 1898.233, 1981.32, 1982.132, 1983.107, 1993.88; A.14378/3503, A.3051; MSCU 004; MTQ 208, 212; JM4701, JM 4703, JM4710, JM4711, JM4717, JM 4728, JM4731, JM4737, JM4738, JM4746; MM1019, NO#3; NJNU 0216; NSMT 24785; ONHM 439, 523, 525, 526, 683, 684, 1015, 1016, 1017, 1020, 1022, 1047, 1050, 1222, 1483, 1557, 1558, 1559, 1560, 1564, 1571, 1572, 1662, 1679, 1911, 1918, 1972, 1973, 2482; OPCF OPC1, SC96-02/06, SC97-03/09, SC97-10/02, SC97-31/05B, SC98-07/08?, SC98-17/04, SC98-17/11, SC99-16/07, SC99-24/12; SC00-04/05, SC00-14/02, SC00-31/07, SC00-30/11, SC01-11/02; PEM 728; EL30; N1049, N1123, N1179, N1219, N1267, N1314, N1364, N1498, N1499, N1567, N1577, N1582, N1593, N1600, N1630, N181, N183, N1950, N1951, N1978, N2059, N2089, N2470, N25, N2766, N472, N533, N534, N544, N825, N826; PNBA BLM09/95, 11/95, 16/95; VST1, VST2; QM J21718, J7443, JM1337, JM14034, JM2149, JM4377, JM5333, JM5355, JM6434; RSLMPC T2, NO#A, NO#C-D; SMNS 45470, 45725, 45727, 45728, 45730, 45731, 45736, 45738, 45739, 45741, 45744, 45745, 45746, 45747, 45748; SMZ 711, NO#A, NO#B, NO#C; SWFSC WFP 0814; TIO S1, S2, S6, S7, S10; USNM 258859, 550939, 550940, 550941; UW NO#; WTCB 3; WTVL 4, 7; WTVT 5; ZAM 1212, 35100, 40944; ZMA 13.319, 13.323, 13.324, 14.597, 19.781, 19.782, 20.721, 20.725, 20.726, 20.727, 20.736, 20.737, 20.738, 20.899, 21.431, 21.437, 21.450, 21.451, 25.221, 25.229; ZRC 4.1572.

## Appendix II

*Museum and Collection Acronyms:* AM, Australian Museum, Sydney, Australia; AMNH, American Museum of Natural History, New York City; BIMS, Bangsaen Institute of Marine Science, Bangkok, Thailand; BMNH, Natural History Museum (formerly the British Museum of Natural History), London, UK; BNHS, Bombay Natural History Society, Mumbai, India; CEPEC, Peruvian Centre for Cetacean Research, Pucusana, Peru; FMNH, Field Museum of Natural History, Chicago, Illinois; IFAN, Institut Fondamental d'Afrique Noir, Dakar, Senegal; JCU, James Cook University, Townsville, Australia; LACM, Los Angeles County Museum of Natural History, Los Angeles, California; LMFRI, Liaoning Marine Fisheries Research Institute, Dalian, People's Republic of China; MNHN, Muséum National d'Histoire Naturelle, Paris; MSCU, Chulalongkorn University, Bangkok, Thailand; MTQ, Museum of Tropical Queensland, Townsville, Australia; NJNU, Nanjing Normal University, Nanjing, China; NMNS, National Museum of Natural Science, Taichung, Taiwan; NSMT, National Science Museum, Tokyo; ONHM, Oman Natural History Museum, Muscat; OPCF, Ocean Park Conservation Foundation, Hong Kong (these specimens have recently been moved to a warehouse under the care of the Agriculture, Fisheries

and Conservation Department, Hong Kong SAR Government); PEM, Port Elizabeth Museum, South Africa; PNBA, Musee, Parc National du Banc d'Arguin, Mauritania; QM, Queensland Museum, Brisbane, Australia; RSLMPC, R. S. Lal Mohan personal collection, Nagercoil, India; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SMZ, Sarawak Museum, Kuching, Malaysia; SWFSC, Southwest Fisheries Science Center (Marine Mammal Synoptic Collection), La Jolla, California; TIO, Third Institute of Oceanography, Xiamen, China; USNM, National Museum of Natural History, Washington, DC; UW, Underwater World, Singapore; WTCB, Cua Be Whale Temple, Nha Trang, Vietnam; WTVL, Vinh Loung Whale Temple, Nha Trang, Vietnam; WTVT, Vung Tau Whale Temple, Vung Tau, Vietnam; ZAM, South African Museum, Capetown, South Africa; ZMA, Zoological Museum, University of Amsterdam; and ZRC, Zoological Record Collection, National University of Singapore, Singapore.

### Appendix III

*Review of Nominal Species:* All nominal species in the synonymy of the genus *Sousa* are listed below:

*Delphinus chinensis* – Osbeck, 1765
The species is based on a description of animals observed by Pehr Osbeck in the Canton (Pearl) River, Guangdong Province, China, in 1751. The original publication date was 1757, but because this was before the initiation of modern taxonomic nomenclature (Linnaeus, 1758), no type specimen was collected. Osbeck's (1765) German translation is, therefore, traditionally used as the official description of the species (see Pilleri, 1979). Porter (1998, 2002) recently designated a neotype specimen, but because the specimen was not described accurately, Jefferson & Karczmarski (2001) suggested that it not be used for representative comparisons. *Sousa chinensis* (Osbeck, 1765) is the senior synonym of the Indo-Pacific humpback dolphin.

*Delphinus malayanus* – Lesson, 1826
Although no type specimen appears to exist (Lesson, 1826), this species has been considered to be synonymous with *Sousa plumbea*. Because other dolphins belonging to the genus *Stenella* were later described under the names *Delphinus* and *Prodelphinus malayanus* (Schlegel, 1841; Weber, 1923), the affinities of the name are controversial. Perrin et al. (1987) reviewed the controversy surrounding this name, and considered it to be a *nomen nudum*, and we concur.

*Delphinus plumbeus* – G. Cuvier, 1829
The type specimen is a skull from "Malabar" (India, Bay of Bengal), housed in the Paris Museum (MNHN A-14378/3503). It was measured by the senior author for this study. Although the current study suggests that *Sousa plumbea* (Cuvier, 1829) may be a good species, its specific validity is still controversial. If not valid, it would be a junior synonym of the Indo-Pacific humpback dolphin (*S. chinensis*).

*Delphinus (Steno?) lentiginosus* – Owen, 1866
The type specimen of this nominal species was captured at "Waltair" (India). It is still in the collection of the Natural History Museum, London (BMNH 1866.2.5.2), where it was measured by the senior author in 1999 as part of this study. This name, *Sousa lentiginosa* (Owen, 1866), is considered to represent a junior synonym of *S. chinensis*.

*Sotalia teuszii* – Kükenthal, 1892
The species is based upon a skull from Cameroon. Hershkovitz (1966) stated that the type specimen was "presumably still in the Jena Natural History Museum"; however, it is actually located in the collection of the Natural History Museum, London (BMNH 1893.8.1.1), where it was recently reexamined by the senior author. This is the senior synonym for what currently is considered the valid species *Sousa teuszii* (Kükenthal, 1892) (Atlantic humpback dolphin), from West African waters.

*Sotalia borneensis* – Lydekker, 1901
Lydekker described the species based upon the skin and skeleton of a dolphin from "Sipang," near the mouth of the Sarawak River, in what is present-day Malaysian Borneo. The Natural History Museum, London, holds the type specimen (BMNH 1901.2.16.1), which was measured by the senior author. Broad consensus exists that *Sousa borneensis* (Lydekker, 1901) is a junior synonym of *S. chinensis*.

*Sotalia fergusoni* – Lydekker, 1903
This species was based on the carcass of a very small (*ca*. 1 m) dolphin collected at "Trevandrum," India. The specimen may have been previously kept in the Trivandrum (Travancore) Museum, but it is now in the collection of the British Museum (BMNH 1903.9.12.2), where it was examined by the senior author. The specimen consists of the skull and postcranial skeleton, obviously of an immature specimen. Based on the illustration in Lydekker (1903), which shows evidence of a dorsal hump, we consider this species to be most

probably synonymous with *Sousa plumbea*, which has date precedence (see above).

*Stenopontistes zambezicus* – Miranda-Ribeiro, 1936
The species was described from a specimen (MN 131) in the Museu Nacional, Rio de Janiero, Brazil, collected in "Zambeze" (presumably Zambezia, in present-day Mozambique, on the east coast of southern Africa). For some time, it was considered erroneously to be a synonym of *Steno bredanensis* (rough-toothed dolphin), but Brownell (1975) reexamined the skull and placed it in the synonymy of humpback dolphins (*Sousa* spp.).

*Sousa huangi* – Wang, 1999
Wang (1999) detailed a young specimen of *Sousa* from Behai, southern China, which he described as a new species, *Sousa huangi*. Huang and Fu (1984) earlier described a specimen from this area, although their work appears never to have been published. Although he did not officially declare a type specimen, Wang (1999) provided a detailed description of the skeleton of the animal at his disposal. His description of the species' "unique" characters is unconvincing, and there is little doubt that any reported differences from *Sousa chinensis* are simply a result of individual and developmental variation. We reject the validity of this species, and provisionally place it in the synonymy of *S. chinensis*.