



## Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia

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### ABSTRACT

The taxonomy of the humpback dolphin genus *Sousa* has been controversial and unsettled for centuries, but recent work indicates that there are several valid species. A review of multiple lines of evidence from skeletal morphology, external morphology, coloration, molecular genetics, and biogeography, in combination provides strong support for the recognition of four species of *Sousa*. These include *S. teuszii* (Kükenthal, 1892), a species with uniform gray coloration and a prominent dorsal hump, which is found in the Atlantic Ocean off West Africa. The species *S. plumbea* (G. Cuvier, 1829) has similar external appearance to *S. teuszii*, but has a more pointed dorsal fin. It occurs in the Indian Ocean from South Africa to Myanmar (Burma). The original taxon, *S. chinensis* (Osbeck, 1765), is reserved for the species that has a larger dorsal fin with no prominent hump, and largely white adult coloration. It ranges from eastern India to central China and throughout Southeast Asia. Finally, we describe a new species of *Sousa*, the Australian humpback dolphin, which occurs in the waters of the Sahul Shelf from northern Australia to southern New Guinea. It has a lower dorsal fin, more extensive dark color on the body, and a dorsal “cape.” It is separated from the Indo-Pacific humpback dolphin by a wide distributional gap that coincides with Wallace’s Line.

**Key words:** taxonomy, systematics, phylogenetics, *Sousa chinensis*, *Sousa teuszii*, *Sousa plumbea*, new species, type description.

Humpback dolphins (genus *Sousa*) are coastal small cetaceans that occur in the eastern Atlantic, Indian, and western Pacific Oceans (Ross *et al.* 1994, Jefferson and Karczmarski 2001, Parra and Ross 2009). The taxonomy of the humpback dolphins has remained unresolved since the late 1700s and early 1800s, when the first species were described, each based on one or two specimens, as was the practice at the time. These dolphins live mostly in areas that are heavily influenced by human activities, yet where there has been relatively little marine mammal research, at least until recently. As a result, most known populations are facing diverse threats to their survival, but at the same time they have been little studied (see Jefferson and Karczmarski 2001, Parra

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and Ross 2009). Even such rudimentary information as the number of species in the genus and basic population/stock structure remains poorly established.

Clarifying the taxonomy of the humpback dolphins has been recognized as a priority in cetology for decades. About 50 yr ago Fraser (1966) reported that the genus *Sousa* required radical revision, but the specimens needed for this purpose were not available. Two recent studies have examined geographic variation in morphometric characters (Ross *et al.* 1996, Jefferson and Van Waerebeek 2004). While the results were largely similar, interpretations differed, with Ross *et al.* (1996) favoring the view of a single, variable species, and Jefferson and Van Waerebeek (2004) concluding that there were probably at least three valid species.

Preliminary molecular genetic work by Cockcroft *et al.* (1997) and Cockcroft and Smith-Goodwin (2002) found somewhat confusing and contrasting patterns that did not mesh well with known morphological differences. These authors supported the view of a single species. Later work using both mtDNA and nuclear markers (Rosenbaum *et al.* 2002, 2003; Frère *et al.* 2008, 2011) began to show some interesting patterns and provided compelling evidence that revision of taxonomy of this genus was needed. More comprehensive, recent work by Mendez *et al.* (2013) used three different lines of evidence (mtDNA, nuclear DNA, and morphometrics) analyzed both for diagnostic characters and in a phylogenetic framework with large samples from throughout the range, and has now provided the clearest picture yet of humpback dolphin taxonomy. That study showed very similar patterns of divergence from the three data partitions, and strongly supported a hypothesis that dolphins from Australia represented a separate species of *Sousa*.

Despite the confusing and sometimes-conflicting results of many of the above studies, all work on the taxonomy of this genus has shown it to be extremely variable, with a great deal of local adaptation in genetic and morphological features. All studies have found differences among regions and types of humpback dolphins, but interpretation of the results has often been difficult, due to methodological issues, small sample sizes, and limited insights provided by examining only a single type of marker (see Rosenbaum *et al.* 2002, Jefferson and Van Waerebeek 2004).

Based on the totality of evidence available to us, with particular emphasis on the recent study by Mendez *et al.* (2013), we provide here a review of humpback dolphin systematics and propose a revision of the genus' taxonomy that reflects currently understood patterns of variation and divergence. We feel that the scientific evidence is adequate to settle many long-standing controversies about the validity of many of the nominal species in the genus. We also describe a new species of humpback dolphin from Australia.

#### HISTORY OF *SOUSA* TAXONOMY

The genus *Sousa* was originally erected as a subgenus of *Steno* by Gray (1866a), and for much of the next century, humpback dolphins were usually listed under the genus *Sotalia*, along with the South American dolphins today known as *Sotalia fluviatilis* and *S. guianensis*. Iredale and Troughton (1934) were the first to use *Sousa* at the generic level and included *S. lentiginosa* and another species now under *Tursiops*. When the important taxonomic papers of Fraser and Purves (1960) and Fraser (1966) later followed this move, the currently known genus of humpback dolphins, *Sousa*, came into common use. However, Hershkovitz (1966) retained all of the nominal species in *Sotalia*, as did some other authors until the last few decades.

Although *Sousa* has in the past been allied with *Sotalia* and *Steno* in a separate subfamily (*i.e.*, Steninae), this appears to have been a flawed hypothesis, based on convergent evolution in morphology. Recent molecular studies clearly associate *Sousa* with the delphinine cetaceans, which currently also includes the genera *Delphinus*, *Stenella*, *Tursiops*, and *Lagenodelphis* (see Perrin *et al.* 2013). There is no known fossil record for *Sousa*.

Although it is often stated that five nominal species of humpback dolphins have been described (see Ross *et al.* 1996, Cockcroft *et al.* 1997, Rice 1998), in fact, a total of nine nominal species of humpback dolphins have been described (not including the many additional name variations and misspellings noted in Hershkovitz [1966], which together make 23 species names). Jefferson and Van Waerebeek (2004) conducted a preliminary review of the history of the taxonomy of the genus, and their discussion of the nominal species is revised and updated below, based on the results of recent work and our current proposal for taxonomic revision of the genus. Museum and collection acronyms are defined in Appendix S1.

#### *Delphinus chinensis* Osbeck, 1765

This species is based on a description of live animals observed by Pehr Osbeck in the Canton (Pearl) River, Guangdong Province, China, in 1751. The original publication date of Osbeck's description was 1757, but no type specimen was provided (Linnaeus 1758) and this was before the starting point of modern taxonomic nomenclature (1 January 1758). The translation of Osbeck's description (1765) into German is therefore traditionally used as the official description of the species (see Hershkovitz 1963, Pilleri 1979). For many years, the detailed description of a specimen by Flower (1870) provided a "surrogate" for an official type specimen, but unfortunately that skeletal material was destroyed in World War II (Pilleri 1979). Porter (1998, 2002) recently designated a neotype and deposited it in the British Museum (Natural History), but because the specimen was not accurately described, it has been suggested that it not be used for comparative purposes (see Jefferson and Karczmarski 2001). *Sousa chinensis* (Osbeck, 1765) is the senior synonym of the Indo-Pacific humpback dolphin, as redescribed below.

#### *Delphinus malayanus* Lesson, 1826

Although no type specimen appears to exist (Lesson 1826), this species has variously been considered to be synonymous with either *Stenella dubia* or *Sousa plumbea* (Hershkovitz 1966). Van Bree (1986) made an argument suggesting that *D. malayanus* would actually have taxonomic priority over *S. 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 with that assessment.

#### *Delphinus plumbeus* G. Cuvier, 1829

The holotype skull from "Malabar" (India, Bay of Bengal), housed in the Muséum national d'Histoire naturelle [Paris Museum] (MNHN A-14378/3503, Robineau 1990), was measured by TAJ for the Jefferson and Van Waerebeek (2004) study. Based on the results of the current investigation (see below), *Sousa plumbea* (G. Cuvier, 1829) is a valid species, and is the senior synonym for the Indian Ocean humpback

dolphin. We resurrect this species here. Figures of the external appearance of the type specimen, showing the prominent dorsal hump, are reproduced in Arvy (1972).

*Delphinus (Steno) lentiginosus* Owen, 1866

The type specimen of this species was captured at “Waltair” (in present-day Visakhapatnam, at about 18°N in central eastern India) (Owen 1866). Hershkovitz (1966) credited the name to Gray (1866b) for reasons that are unclear. The type is still in the collection of the Natural History Museum, London (BMNH 1866.2.5.2), where it was measured in 1999 as part of the Jefferson and Van Waerebeek (2004) study. The affinity of the type specimen of *S. lentiginosa* (Owen, 1866) has been difficult to ascertain, as it was collected within the range of both the *plumbea*-type and the *chinensis*-type. The plate illustrating the external appearance of the 2.4 m specimen in Owen’s paper shows extensive spotting on the body, but does not give a strong indication of the prominent dorsal hump that is characteristic of the *plumbea*-type, although there is indeed evidence of a keel at the posterior of the dorsal fin (Fig. 1). An illustration of the putative species from Lydekker (1908) (Fig. 1) clearly shows a dorsal hump. Fraser (1966), noting that a taxonomic review of humpback dolphins was “badly needed,” conducted a detailed examination and his analysis appeared to support Lydekker’s (1908) suggestion that *S. lentiginosa* is most likely allied with the *plumbea*-type and not the *chinensis*-type. Thus, we consider that this name represents a junior synonym of *Sousa plumbea*. The possibility still exists that this form represents an intermediate (hybrid) between *S. plumbea* and *S. chinensis*, but the current molecular data do not seem to support this supposition, although it should be noted that the sample size from the area of known sympatry is small (Mendez *et al.* 2013).

*Sotalia teuszii* Kükenthal, 1892

The species is based upon a skull from Cameroon, West Africa. 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

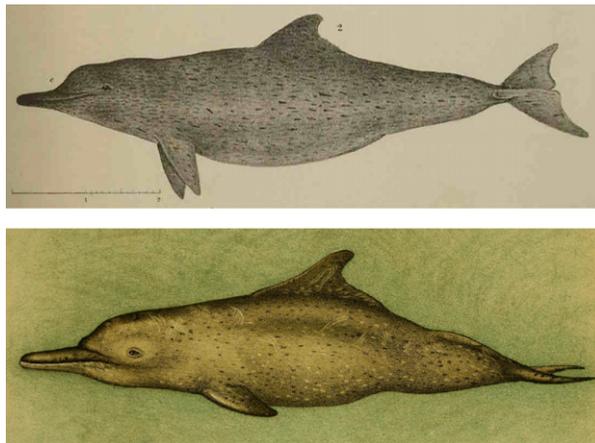


Figure 1. The type specimen of *Delphinus lentiginosus* Owen, 1866 (upper), and illustration of the putative species from Lydekker (1908) (lower) showing a dorsal hump.

Museum, London (BMNH 1893.8.1.1), where it was reexamined by one of us, TAJ (for Jefferson and Van Waerebeek 2004). This is the senior synonym for what is considered the valid species *Sousa teuszii* (Kükenthal, 1892) (Atlantic humpback dolphin), from West African waters. Illustrations of the skull were not published with the type description, but Pilleri and Gahr (1972) provided photographs of the type specimen.

*Sotalia borneensis* Lydekker, 1901

Lydekker (1901) described this 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 for Jefferson and Van Waerebeek (2004). Broad consensus has existed that *Sousa borneensis* (Lydekker, 1901) is not valid, and is a junior synonym of *S. chinensis* (see Jefferson and Van Waerebeek 2004), and we currently consider it to be in the synonymy 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 as part of the Jefferson and Van Waerebeek (2004) study. The specimen consists of the skull and postcranial skeleton, of an obviously immature specimen. Based on the illustration in Lydekker (1903), which shows an apparent dorsal hump, we consider this species to be a junior synonym of *Sousa plumbea*.

*Stenopontistes zambezicus* Mirando-Ribiero, 1936

The species was described from a specimen (MN 131) in the Museu Nacional, Rio de Janeiro, Brazil, collected in "Zambezi" (presumably Zambezia, in present-day Mozambique, on the east coast of central/southern Africa). For some time, it was erroneously considered 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.). We agree, and notwithstanding the protests of Pilleri and Gahr (1976), we consider it to be a synonym of *S. plumbea*.

*Sousa queenslandensis* Gaskin, 1972

Gaskin (1972) surmised that Australian humpback dolphins might eventually be found to be a separate species or subspecies, and proposed the name *Sousa queenslandensis* if that were indeed found to be the case. But, as no biological description of characters that would differentiate the taxon were provided by Gaskin, this name violates Article 13 of the International Code of Zoological Nomenclature (ICZN 1999), is considered to be a *nomen nudum*, and is therefore not available.

*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) had earlier described a specimen from this area in an abstract, and 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 (see Jefferson *et al.* 2012 for a description of the age- and sex-related variation of these animals). We reject the validity of this species, and firmly place it in the synonymy of *S. chinensis*.

#### *Recent and Current Nomenclature*

In the last 50 yr, several global lists of marine mammal species have been published, and these have generally been used to summarize the prevailing views on marine mammal taxonomy at the time. The first of these, by Scheffer and Rice (1963), listed five species of humpback dolphins, all under the genus *Sotalia* (*S. chinensis*, *S. borneensis*, *S. lentiginosa*, *S. plumbea*, and *S. teuszii*). Scheffer and Rice (1963) also noted that the taxonomy of this group was in need of revision, a notion that has often been echoed in later literature on humpback dolphins. Hershkovitz (1966), in his exhaustive review of cetacean taxonomy, recognized the same five species, still under *Sotalia*. Rice and Scheffer (1968) listed all the same species, but moved them to the genus *Sousa*. Later, Rice (1977) only listed *S. chinensis* and *S. teuszii*, and noted that *teuszii* might possibly be a subspecies of *chinensis*. In the most recent definitive such list, Rice (1998) listed three species, *S. teuszii*, *S. plumbea*, and *S. chinensis*. For many years, the International Whaling Commission's list of cetacean species, which is often viewed as a *de facto* official list, has listed only two species (*S. chinensis* and *S. teuszii*). However, the Society for Marine Mammalogy's Ad Hoc Committee on Taxonomy (Committee on Taxonomy 2014) has recently split *Sousa chinensis* into three species, as recommended by Mendez *et al.* (2013).

### SUMMARY OF EVIDENCE FOR MULTIPLE SPECIES

#### *Skeletal Morphology*

The first comprehensive study of *Sousa* cranial morphometrics was conducted by Jefferson and Van Waerebeek (2004), using skulls of 222 specimens from throughout virtually the entire known range of the genus. They found strong evidence for separate species status for *S. teuszii*, which has significantly lower tooth counts (an average of about 30 teeth per row *vs.* about 33–37 for other areas; Fig. 2) and a shorter, wider skull (length/breadth ratio averaging 2.28 *vs.* 2.37–2.49 for the other species; Table 1). Principal Components Analysis (PCA) results also separated *S. teuszii* specimens well. This study also provided preliminary evidence for the separation of *S. plumbea* from *S. chinensis*, due to higher length/breadth ratios of the skull and partial separation in PCA analyses; see Fig. 3), although the authors suggested awaiting further work to make any taxonomic revisions. While in general, patterns of cranial variation were conservative, there was great variability in condylobasal length (CBL) among different areas, perhaps reflecting local adaptation. One obvious example was from the Indian Ocean, where Persian Gulf skulls were much smaller than those from relatively nearby India (Jefferson and Van Waerebeek 2004). Ross *et al.* (1996) found many similar patterns, based on smaller sample sizes, but interpreted these as regional variations largely below the species level.

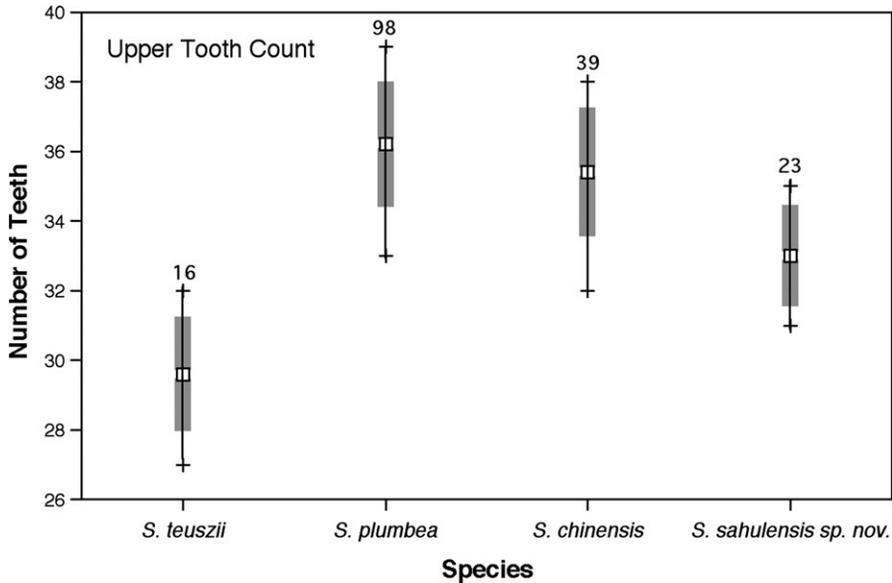


Figure 2. A comparison of tooth counts for the different species of *Sousa*. Squares are means, shaded boxes are  $\pm 1$  SD, and vertical bars are ranges. Sample sizes are given above each bar.

Mendez *et al.* (2013) have completed the most recent and complete analysis, largely based on the Jefferson and Van Waerebeek (2004) data set, with the addition of a few more specimens. Mendez *et al.* conducted a new multivariate analysis (Canonical Correspondence Analysis), which showed patterns very similar to those described from molecular markers (discussed below). In their morphological analysis, specimens from West Africa, China, Australia, and Southeast Africa all separated out quite distinctly on a plot of Canonical Scores 1 and 2. Specimens from India, Oman, and Thailand/SE Asia showed substantial overlap with each other, but separated out from the areas listed above. This is seen as supporting (or at least consistent with) the separation of *S. teuszii* and Australian specimens as distinct species (see Mendez *et al.* 2013 for more details).

Although based on very small sample sizes, there is some preliminary evidence for differences in vertebral counts among the putative species (Fig. 4). Atlantic humpback dolphins would appear to have more vertebrae (52–53) than for western Indian Ocean humpback dolphins (49–51), and appear to overlap the number for Chinese humpback dolphins (50–53), though with possible modal differences. Vertebral data from Australian humpback dolphins suggest that they typically have only 50 total vertebrae. There also appear to be some differences in counts by vertebral region, with western Indian Ocean humpback dolphins having fewer thoracic and caudal vertebrae than animals from Southeast Asia (see below). However, these apparent differences need to be confirmed with larger data sets.

#### *External Morphology*

No study has been able to adequately examine geographic variation in external morphology, because there are few data sets of systematically measured fresh specimens for

Table 1. Summary of cranial morphometrics (in mm) and meristics for the four species of *Sousa*, based on adult specimens (except for tooth counts, which are based on all specimens).

Measurement	<i>S. teuszii</i>				<i>S. plumbica</i>				<i>S. chinensis</i>				<i>S. sabulensis</i>			
	Mean	±SD	Range	n	Mean	±SD	Range	n	Mean	±SD	Range	n	Mean	±SD	Range	n
Upper tooth count	29.6	1.41	27–32	16	36.2	1.57	33–39	98	35.4	1.62	32–38	39	33.0	1.23	31–35	23
Lower tooth count	28.4	1.02	27–31	10	34.5	1.44	31–37	78	33.0	2.00	29–38	40	32.8	0.80	31–34	26
Tooth diameter	6.40	0.711	4.9–7.4	12	5.97	0.470	4.8–6.9	67	6.13	0.678	4.7–7.8	27	6.60	0.400	6.0–7.2	13
Condylabasal length	494.7	10.10	481–511	13	520.9	26.96	457–595	80	507.3	18.45	466–536	28	507.9	17.47	482–554	14
Length of rostrum	294.9	8.15	279–308	14	322.2	20.22	276–377	81	309.1	16.17	277–339	31	308.6	14.78	287–350	13
Width of rostrum at base	114.5	4.94	107–127	15	107.5	8.04	90–131	82	109.7	5.30	96–117	39	109.1	5.35	99–118	15
Width of rostrum at 1/2 length	48.9	2.77	44–54	14	46.0	3.17	37–55	78	46.4	3.20	40–55	32	46.6	2.35	44–52	14
Width of rostrum at 3/4 length	34.1	3.01	28–38	15	32.7	2.84	27–41	78	32.0	2.35	29–38	30	32.9	2.58	30–38	14
Width of premax. at 1/2 length	33.6	3.91	27–44	15	29.3	3.31	21–39	78	28.9	3.03	23–37	32	31.0	2.00	28–37	14
Greatest width of premax.	85.9	2.40	83–90	15	80.8	5.32	70–93	85	82.7	3.66	73–91	37	76.7	3.05	72–83	15
Preorbital width	199.1	5.03	192–210	15	186.4	12.04	159–219	79	190.3	8.11	170–200	37	184.6	7.54	169–197	14
Postorbital width	223.6	24.59	209–312	16	210.7	14.26	176–244	77	213.0	8.18	192–226	38	210.8	8.33	196–226	14
Zygomatic width	217.1	6.86	209–239	16	207.8	14.48	177–243	85	213.8	8.54	192–224	37	211.7	9.40	195–230	15
Parietal width	162.7	15.14	142–183	15	154.4	8.56	133–175	85	145.7	5.61	136–158	34	145.6	5.00	136–155	15
Width of external nares	53.5	4.47	44–60	15	53.0	2.99	46–60	85	54.6	3.21	47–63	37	50.6	1.71	48–54	15
Width of internal nares	61.1	7.02	46–72	15	60.4	3.92	52–70	80	66.1	5.45	53–74	37	61.2	3.27	56–68	15
Length of temporal fossa	104.7	3.57	97–111	16	105.3	7.68	84–125	82	111.7	4.50	101–121	36	108.5	4.84	100–117	15
Height of temporal fossa	81.4	12.54	53–98	16	83.2	6.48	66–98	84	87.2	4.85	75–98	36	90.4	5.41	83–99	15
Length of orbit	55.5	2.42	51–59	15	56.8	3.20	49–65	81	56.1	2.23	51–63	37	56.5	2.06	52–61	15

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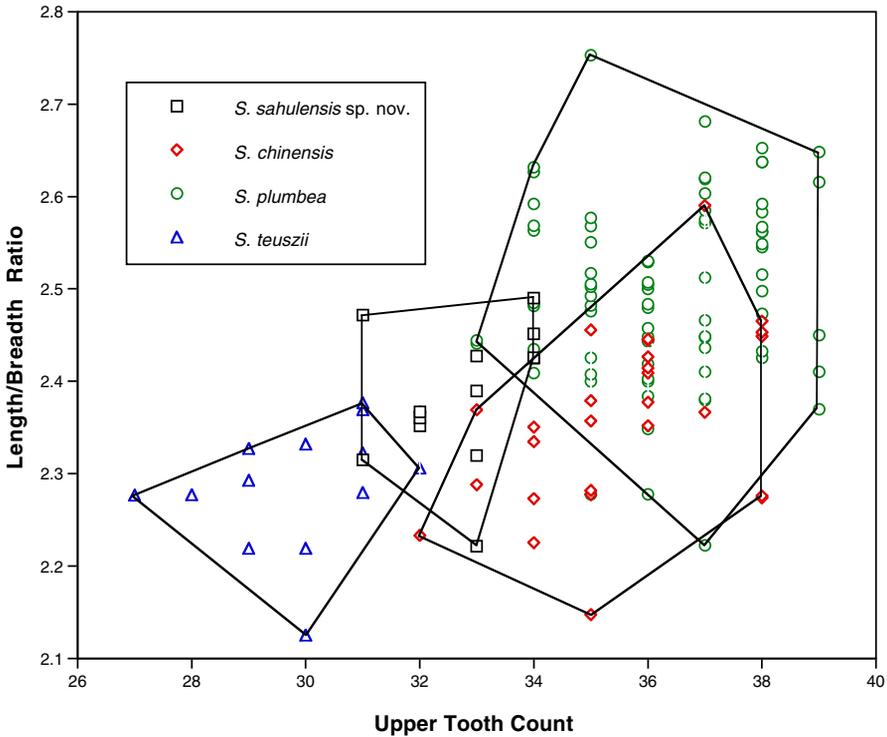


Figure 3. Upper tooth count vs. length/breadth ratio of the cranium, showing partial separation of the four species of *Sousa*.

comparison. It is apparent that, with available measurements coming mostly from stranded specimens and measured by a wide variety of researchers, poor data quality and interobserver variability would likely mask any real differences that might exist. Nonetheless, there are clearly differences (be they absolute or modal) in various external features of humpback dolphins from different areas. Ross *et al.* (1994) compiled available external morphometric data and provided some suggestion of regional differences in total length. Indian humpback dolphins may reach larger total lengths than those from other parts of the range, as evidenced by scant data from the literature (reviewed in Ross *et al.* 1996; see Fig. 5) and by their relatively large skulls, by far the largest of any measured for the genus (see Jefferson and Van Waerebeek 2004).

One of the most obvious of these differences is in the form of the dorsal fin. In specimens from the western part of the range, that is the Atlantic Ocean and Indian Ocean east to the Bay of Bengal, the small, falcate dorsal fin sits atop a lengthened and thickened hump of connective tissue on the back (the “hump” that is referred to in the common name). This dorsal hump may reach up to 39% of the total length in animals from western and southern Africa (Ross *et al.* 1996). The dorsal structure (*i.e.*, the hump, if present, and dorsal fin) ranges from 26% to 32% of total length in *S. teuszii* (Cadenat 1956, 1959; Cadenat and Paraiso 1957), 23% to 38% of total length in *plumbea*-type dolphins (Ross 1984, Best 2007), and 15% to 21% in *chinensis*-type dolphins (Zhou *et al.* 1980; TAJ, unpublished). On the other hand, the dorsal fin itself tends to be larger and more triangular, and the hump is absent in specimens from the

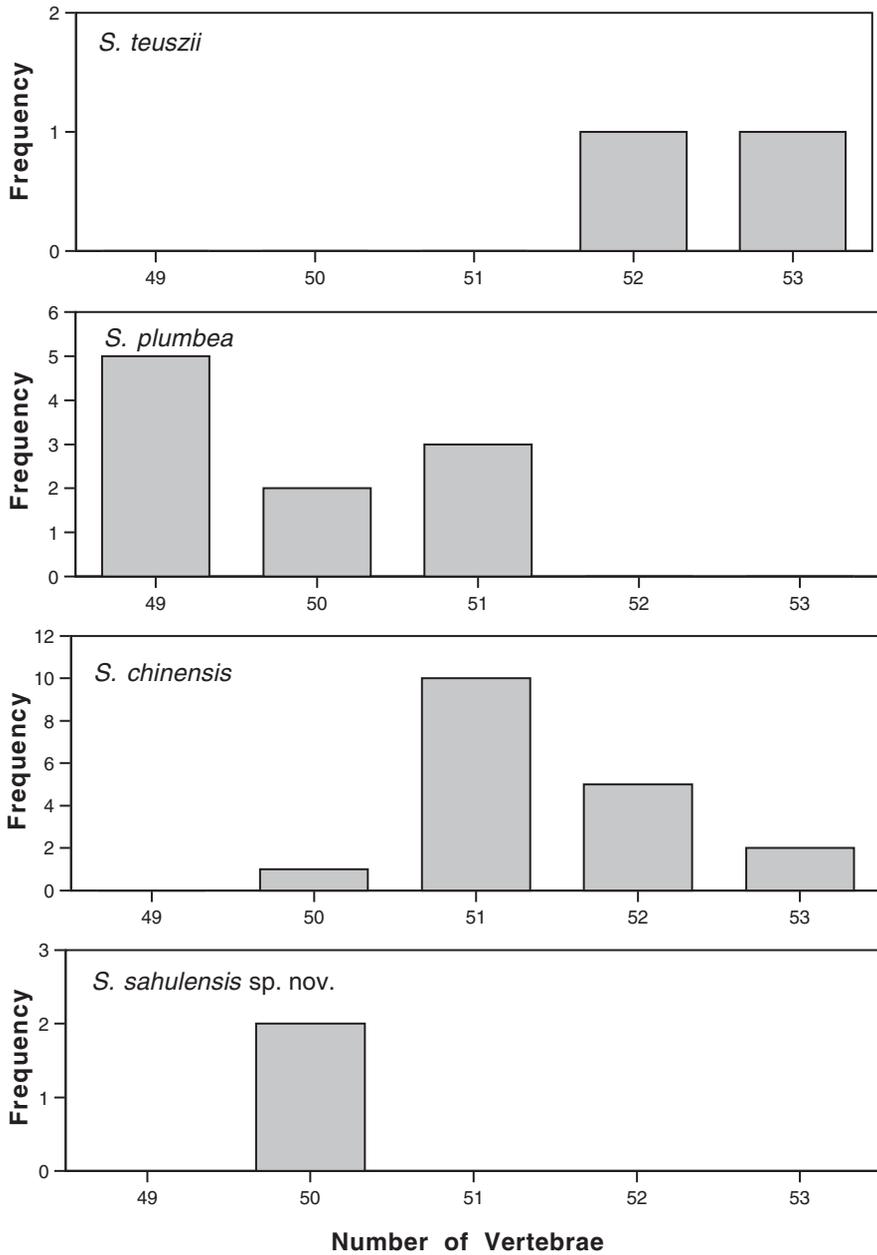


Figure 4. Histograms of total vertebral counts for the different species of *Sousa*.

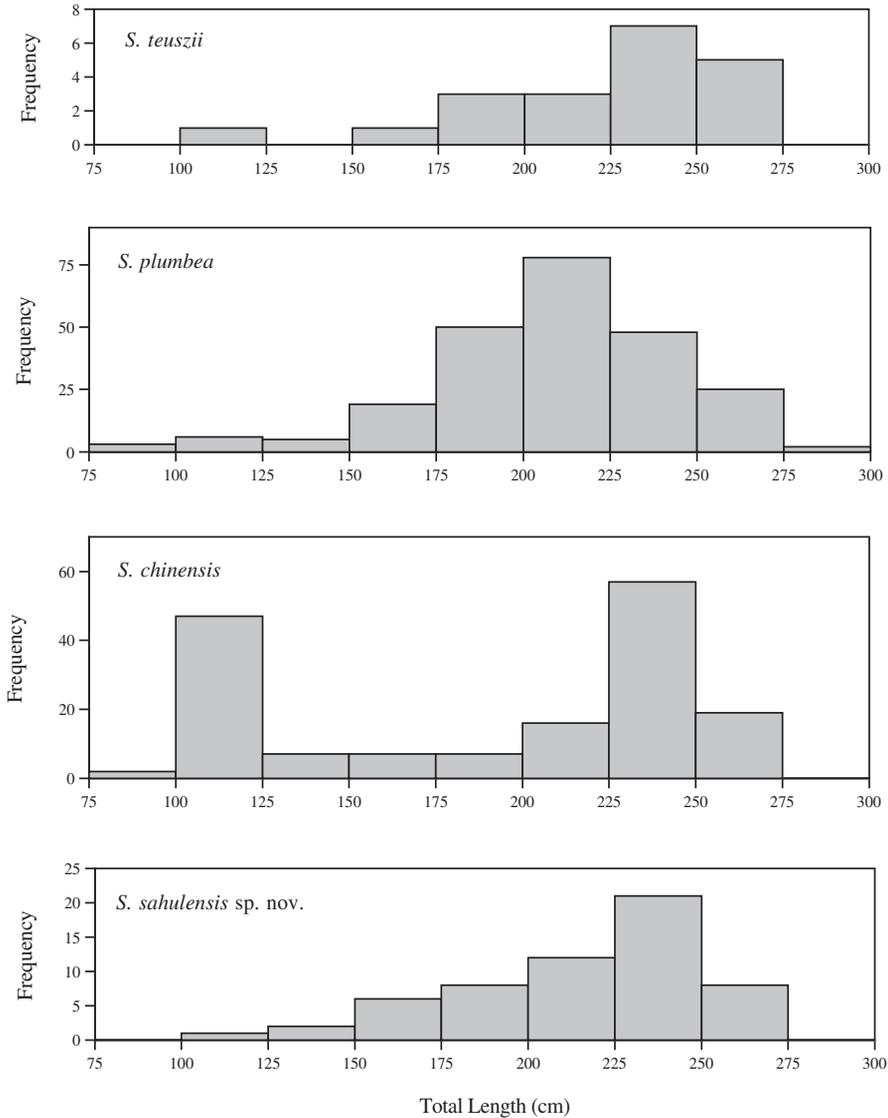


Figure 5. Histograms of total length for the four different species of *Sousa*. Data are from the literature and TAJ's unpublished records.

eastern part of the range, those from Southeast Asia east to central China and the northern parts of Australia (see Jefferson and Karczmarski 2001 for a description).

There is also evidence that the dorsal fin of humpback dolphins from equatorial and Southern Hemisphere waters in Southeast Asia can be extremely low and wide-based, with a very triangular shape. However, there are very few quantitative data available on this, and most of these allegations have been made from single specimens (including the type of *S. borneensis*; Lydekker 1901, see Ross *et al.* 1996 for a discussion), which may have been aberrant in some cases. Addi-

tionally, Atlantic humpback dolphins have relatively shorter beaks than the other species (Jefferson and Van Waerebeek 2004).

### *Coloration*

Few systematic studies of *Sousa* coloration have been published, and many descriptions of coloration in humpback dolphins are based on single specimens, often not in a fresh condition, and thus must be viewed with some level of skepticism. There is also extensive age-related and sexual variation in coloration (see, for example, Jefferson *et al.* 2012), and these types of variation have often not been clearly separated from geographic variation in past studies. For instance, it appears that young calves and juveniles are dark gray in all forms/species of the genus.

The color patterns of humpback dolphins in the western portion of the range (*i.e.*, those that have the prominent hump) tend to be rather similar, with adults showing more-or-less monotone dark brownish gray coloration, but with older animals often having areas of white around the dorsal fin and tail stock. However, animals from southern Africa are somewhat lighter ventrally than those from Tanzania/Kenya or the Arabian region.<sup>2</sup> Humpback dolphins in the eastern portion of the range (*i.e.*, from the Bay of Bengal to the east) have a very different pattern in which young animals that are generally countershaded gray lose much or all of their pigmentation as adults and may become mostly white (often with a pinkish tinge, caused by blood flushing) in old age (see description in Ross *et al.* 1996). This pattern has been described in detail from multiple specimens of all age classes by Jefferson *et al.* (2012) for the population in Hong Kong and the Pearl River Estuary. There is some element of sexual dimorphism in this population, with females losing their pigmentation earlier than males, and older adult females are often completely white in color (pinkish hues are common). Most *chinensis*-type humpback dolphins (*i.e.*, those without the prominent dorsal hump) have a broadly similar color pattern, but they generally appear to retain more of their dark pigmentation (either in the form of dark blotches or spotting/flecking) into old age, than those in Chinese waters.

Australian humpback dolphins have a color pattern component apparently not found in any other humpback dolphins, *i.e.*, that is an indistinct diagonal separation of the dark upper body and lighter belly/lower sides (see Fig. 6). This “cape” margin sweeps above the eye, reaches its highest point on the neck area, and then slants downwards to meet the urogenital area. It often has an oval invasion of light color from below, at the level of the dorsal fin. Australian humpback dolphins often have uneven blotches of white/pink on their bodies, but while still retaining large patches of dark pigmentation or dark spotting/flecking into old age (see Ross *et al.* 1996 for a description).

### *Genetics and Phylogenetic Relationships*

There is no known fossil record for the genus. While recent published phylogenetic studies on the genus *Sousa* have been constrained by the small number of samples available from the entire range and/or the use of a single genetic marker (*e.g.*, Frère *et al.* 2008, 2011; Lin *et al.* 2010), their conclusions have consistently called for some type of distinction of animals from Southeast Asia and Australia. In 2008

<sup>2</sup>Personal communication from V. G. Cockcroft, Centre for Dolphin Studies, Box 1856, Plettenberg Bay, 6600, South Africa, 2014.



Figure 6. The external appearance of the Australian humpback dolphin, showing the diagnostic dorsal cape: adult-sized specimen porpoising at sea (upper), and mother/calf porpoising at sea (lower). Photographs by R. L. Pitman (upper) and G. J. Parra (lower).

Frère *et al.* (2008) conducted an analysis of the genus *Sousa* using a 338bp mitochondrial DNA control region sequence from 72 *Sousa* specimens representing three putative populations in the Indo-Pacific (South Africa: *S. plumbea*,  $n = 23$ ; China: *S. chinensis*,  $n = 19$ ; and Australia: *S. chinensis*,  $n = 28$ ), and *S. teuszii* in the Atlantic (Mauritania,  $n = 2$ ). While all three populations formed monophyletic groups, animals from South Africa and China grouped with *S. teuszii*, rather than with animals from Australia. These results were wholly based on the limited sampling of *Sousa* throughout their range for mtDNA only, and the detected patterns were similar in nature and results to those of Rosenbaum *et al.* (2002, 2003). Frère *et al.* (2011) conducted an analysis based on a total of 33 samples, yielding 5 mtDNA haplotypes from Australian animals, 10 mtDNA haplotypes from the *chinensis*-type and one mtDNA haplotype from West Africa. Based on this limited level of sampling, the combined mtDNA and nuDNA data sets focused principally on an analysis of samples from Hong Kong and Australia, revealing a total of three genetic types (one from Australia, and one from China, and one from Indonesia). As Frère *et al.* (2011) did not include morphological characters and lacked samples from large stretches of the known *Sousa* range (*e.g.*, southwestern and northern Indian Ocean), there are limited comparisons to the Frère *et al.* (2008) findings and the results were insufficient to definitively characterize the nature and level of variation (*i.e.*, population, subspecies, or species level) observed for animals off Australia, as well as for putative species in other parts of the range.

In the most comprehensive study of *Sousa* taxonomy to date, Mendez *et al.* (2013) recently presented a combined genetic and morphological analysis of humpback dolphins from throughout their existing range, and used a comprehensive set of analytical methods to explore the data. From this study, the most comprehensive sampling and robust evidence to revise taxonomy in the genus *Sousa* was presented, including diagnostic mtDNA and nuDNA characters, clear-cut phylogenetic patterns using all molecular evidence, and morphological data (that was concordant with four species designations hypothesized from both morphology and genetic information).

Based on a total of 235 samples from free-ranging members of extant populations, beach-cast and museum specimens throughout their range, Mendez *et al.* (2013) analyzed data from the mitochondrial control region and four nuclear introns, which included character-based, phylogenetic, population-level, and population aggregation analysis (PAA) frameworks. In addition, 180 samples from the same geographical locations allowed comparisons of 24 morphological characters through multivariate analyses. The nuclear data set displayed clear evolutionary divergence (assessed through rigorous phylogenetic analyses) for the four species assemblages proposed, with the mtDNA data set showing even stronger differentiation. In total, Mendez *et al.* (2013) revealed that the geographies studied (West Africa, Southeast Africa, Arabia-Oman, the Indian subcontinent, Thailand, China, and Australia) “exhibited extreme and significant differentiation in our analysis of genetic structure and shared no mtDNA haplotypes, formed well-resolved clusters in the phylogenetic analyses when considering nuDNA and mtDNA jointly and separately, are diagnosable under the PAA approach and exhibited statistically significant morphological differentiation (with the exception of Arabia-Oman, the Indian subcontinent, and Thailand, which formed a single cluster)” (Fig. 7). All mtDNA haplotypes were exclusive to the putative species and the data set revealed a greater number of diagnostic characters than the nuDNA. The putative species were diagnosable largely by mtDNA characters, as well as nuDNA characters (one diagnostic character diagnoses *teuszi* and *plumbea* samples from the other putative species; see Table 2), suggesting that they represent separate species under the Phylogenetic Species Concept. From a combined “tree-based” or clustering approach for the molecular data sets, the largely congruent

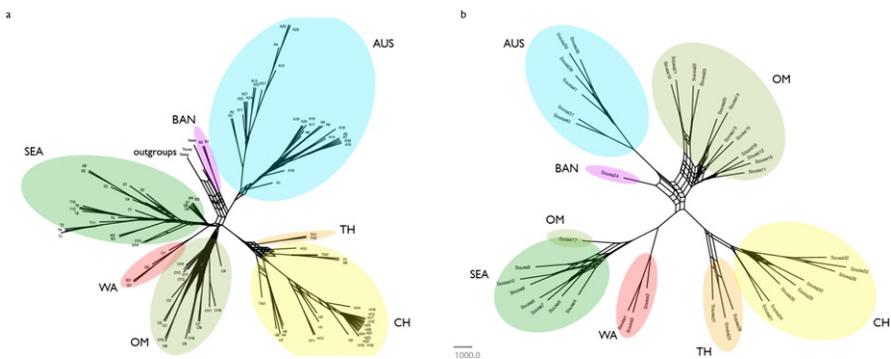


Figure 7. Molecular consensus networks from 100 maximum likelihood (ML) phylogenetic tree inferences and 2,000 bootstrap pseudoreplicates: concatenated mtDNA and nuDNA data sets (left), and mtDNA data set (right). Geographic abbreviations: WA (West Africa), Southeast Africa (SEA), Oman (OM), Indian subcontinent (IN), Thailand (TH), China/Hong Kong (CH), Australia (AUS). From Mendez *et al.* (2013).



results revealed the existence of five assemblages that are evolutionarily unique: (1) West Africa, (2) Southeast Africa, (3) Arabia, (4) China, and (5) Australia. From a phylogenetic perspective of the combined nuclear and mtDNA datasets, *S. chinensis* shows a closer relationship with the new species sampled from Australia. *S. plumbea* is paraphyletic, with *S. teuszii* being more closely related to the *S. plumbea* assemblage predominantly from Southeast Africa. The mtDNA phylogenetic analysis also revealed paraphyly for *S. plumbea* lineages. Additionally, the relationship between Southeast Africa and Arabia samples, as revealed by one mtDNA haplotype from Oman clustering with those from Southeast Africa may not be fully resolved with incomplete maternal lineage sorting (see fig. 7 in Mendez *et al.* 2013). Taken in totality, the congruence of results based on the combined genetic and morphological analyses (summarized on p. 9–10 of Mendez *et al.* 2013), provided strong evidence for at least four species within the genus (*S. teuszii*, *S. plumbea*, *S. chinensis*, and a new species from Australia).

#### *Sympatry of plumbea- and chinensis-types*

Previous genetic studies suggested that the *plumbea*- and *chinensis*-types diverged very early in delphinid evolution, about 5.3–10.5 MYA (Cockcroft and Smith-Goodwin 2002). However, the coloration patterns typically attributed to the *plumbea*- and *chinensis*-types of *Sousa* and described above suggest that they currently overlap in distribution in the Bay of Bengal. Dolphins exhibiting the coloration typically associated with the *chinensis* form occur as far west as western Bangladesh (Smith *et al.* 2008) and Orissa, India (Sutaria and Jefferson 2004); in both cases the evidence is supported by excellent photographs. The coloration form typically associated with the *plumbea* type is known to extend to the east as far as the Mergui Archipelago, Myanmar (Burma) (Smith and Tun 2008, supported by photographs), and Great Coco Island, Myanmar (Leatherwood and Clarke 1983; no photographs exist, but detailed descriptions of the dorsal hump leave little doubt). Reports that animals exhibiting the *plumbea*-type coloration range further south and east, to as far as Phuket, Thailand, and Langkawi, Malaysia, are more questionable, as there are no photographs or detailed descriptions to support these (L. Rajamani in Jefferson and Van Waerebeek 2004). These may be misidentifications, as photographs we have seen of humpback dolphins from these areas present coloration types typically associated with the *chinensis*-type animals (as evidenced by the lack of a hump), but they appear to have more extensive dorsal gray coloration than other populations of the *chinensis*-type, and so may have appeared similar to *plumbea* to some observers.

Although Smith and Tun (2008) noted that *plumbea*-type dolphins off the Mergui Archipelago appeared to have a relatively weakly developed dorsal hump, their photograph nonetheless shows animals with a distinct hump. There is extensive geographic, sexual, and age-related variation of the development of the dorsal hump in *plumbea*-type dolphins (see Ross *et al.* 1994, 1996). However, at this point, there is no convincing evidence of hybridization/intergradation of the two types in this area of sympatry. The sample analyzed from Bangladesh in Mendez *et al.* (2013), however, was highly distinct from samples considered *plumbea*-type, *chinensis*-type, and the animals from Australia. Overall, there is a paucity of specimen material available from this apparent area of overlap, and future sampling from this region should be considered a priority to confirm the relationships and taxonomic affinities for these humpback dolphins.

THE EXISTENCE OF AN AUSTRALIAN SPECIES OF *Sousa*

The possibility of a distinct species of humpback dolphin in Australian waters was first mentioned by Gaskin (1972), and he even proposed the name *Sousa queenslandensis* for the species if it were indeed found to be distinct. However, because there was no biological description or type specimen provided by Gaskin, this name is not available for the new species of *Sousa*. The name violates Article 13 of the International Code of Zoological Nomenclature (ICZN, 1999), and thus must be considered to be a *nomen nudum*.

Evidence that genetically distinct humpback dolphins are found in Australian coastal waters has been accumulating for some years. This has mainly come from molecular studies, which have used mtDNA to show a long-term separation of humpback dolphins in Southeast Asia from those in Australia, and some later work adding nuclear markers supported this and additional molecular evidence (Rosenbaum *et al.* 2003; Frère *et al.* 2008, 2011). However, due to limited sampling, analyses of only a single genetic marker (mtDNA), and focussed comparisons involving a subset of the variation known to exist within the genus, the previous studies could not fully or definitively ascribe the levels of genetic differentiation detected (*i.e.*, population, subspecies, or species) for the Australian-sampled animals. Recent work combining molecular and morphometric data sets added multiple lines of evidence to evaluate taxonomy within the genus *Sousa* (Mendez *et al.* 2013), which solidified the conclusion of a separate species that is currently known from the coastal waters of Australia and Papua New Guinea. One scenario, based on mtDNA results only, suggested that the genus *Sousa* originated in eastern Australia and radiated northwards and westwards in a complex fashion over the last 8.02 MY (Lin *et al.* 2010). There is no known fossil record for the genus *Sousa*, but the report by Whitmore (1987) of a fossil periotic bone (>15 MY old) from a species closely related to *Sousa* is consistent with the hypothesis that *Sousa* has a long evolutionary history, and evolved early in delphinid evolution.

It is perhaps not surprising that the divergence between the Australian species and *S. chinensis* appears to occur along Wallace's Line. Wallace's Line has long been known to be an important biogeographic boundary for many plants and animals. This is true, in particular for terrestrial mammals, largely due to the long distance that separated Asia and Australia throughout much of recent evolutionary history (see Raven 1935). However, the line was thought to be primarily a factor in evolution of terrestrial organisms. A somewhat-surprising recent finding was that Wallace's Line also can apply to marine organisms. Barber *et al.* (2000) showed that there were sharp genetic breaks along Wallace's Line in a variety of coral reef organisms, and Sulaiman and Ovenden (2010) demonstrated that it can even apply to relatively mobile fishes, such as mackerel.

The first evidence that Wallace's Line may apply to cetaceans as well was provided by Beasley *et al.* (2005), who found strong evidence that dolphins of the genus *Orcaella* (previously all considered to be *O. brevirostris*) had split into separate species on either side of a distributional gap along Wallace's Line (*O. brevirostris* in Southeast Asia and *O. beinsobni* in Australia and New Guinea).

Humpback dolphins, like *Orcaella* spp., are coastal, shallow-water animals and it appears likely to us that for both these genera, speciation along Wallace's Line has less to do with the large distances separating these land masses in the geologic past and more to do with the relatively deep water that has long separated Southeast Asia from Australia/New Guinea. Humpback dolphins do not generally occur around oceanic islands separated from the mainland by expanses of deep water, such as around

Mauritius or the Maldives. The Sunda Shelf of Southeast Asia extends around Sumatra, Java, and Borneo. The Sahul Shelf surrounds Australia and connects it to the island of New Guinea. Between these shallow shelves, waters are deep and drop off quickly from the shoreline. Voris (2000) provided maps showing sea levels in this area over the past 17,000–250,000 yr; and even during time periods with substantially lower sea levels than at present, there was a significant region of deep water in the Moluccas/Banda Sea/Timor Sea area. This region of deep water presumably represented unsuitable habitat, and thus a barrier to dispersal of shallow-water cetaceans such as dolphins of the genera *Orcaella* and *Sousa*. During the last glacial maximum ca. 18,000 yr ago the Sahul and Arafura shelves (around Southeast Asia and Australia/New Guinea) were exposed as dry land (see Voris 2000). Therefore, as the water level increased *Sousa* was able to move from New Guinea to Australia and *vice versa*. Alternatively, the movement may have happened at some earlier period, as sea levels changed many times during the past two million years, but regardless of the timing, the shallow waters of the Sahul Shelf allowed *Sousa* and *Orcaella* to disperse to/from Australia. This may explain the patterns of species distributions that we see today in both those groups.

Humpback dolphins (consistent with the *chinensis*-type) are well known from the western part of the Indo-Malay archipelago, with many well-documented records from Singapore, Peninsular Malaysia, Malacca Straits/Sumatra, and the island of Borneo (see Mörzner Bruyns 1971, Beasley and Jefferson 1997, Rudolph *et al.* 1997). A small number of *Sousa* sightings have been reported for Komodo Island in the central part of the archipelago, although these are not supported by photographs or detailed descriptions, and therefore may be considered unconfirmed (Kahn and Pet 2003). In fact, the description of the animals as all gray in color makes us suspect that these may be misidentifications. Other than these records, we have been unable to find any records of humpback dolphins from the more eastern Indonesian islands (*i.e.*, Sulawesi, the Moluccas, islands of the Savu Sea, Solor/Alor, Timor, or the Lesser Sunda Islands). This is despite fairly extensive cetacean field work associated with the cetacean fisheries of the Savu Sea at Lamalera and Lamakera (*e.g.*, Hembree 1980; Barnes 1980, 1991; Rudolph 1993; Mustika 2006), as well as other cetacean survey work at Sulawesi (Rudolph 1999), Solor/Alor (Kahn 2003), and in the northern Arafura/Timor seas (Porter and Chilvers 2003, Borsa and Nugroho 2010). As one moves further east, humpback dolphin records are again to be found from the southern Timor and Arafura seas (Rudolph *et al.* 1997, Porter and Chilvers 2003), but these are waters associated with the Australian continental (Sahul) shelf. We suggest that there is a large distributional gap in the area of eastern Indonesia (*i.e.*, the Molucca Ceram, Savu, and northern Timor seas), separating *S. chinensis* from Australian humpback dolphins, where deep water occurs immediately offshore of land (see Voris 2000), and does not provide suitable shallow-water habitat for humpback dolphins. The Timor Trough between the Indonesian island of Roti and the Sahul Bank is approximately 2,000 m deep (Whiting 1999), much deeper than humpback dolphins would occur in. This would potentially act as a present-day barrier to *Sousa* dispersal. *Sousa* thus appears to be associated with the Sunda Shelf in Southeast Asia (*S. chinensis*) and the Sahul Shelf around Australia and New Guinea (Australian species), but not with the deep waters between these shelves. However, only detailed cetacean survey work in this area will confirm or refute this hypothesis.

## SPECIES DESCRIPTIONS AND TAXANOMIC TREATMENT

Order Cetartiodactyla Montgelard, Catzefils and Douzery, 1997

Cetacea (Brisson, 1762)

Family Delphinidae Gray, 1821

Genus *Sousa* Gray, 1866a

Based on the information reviewed above, we propose the recognition of four valid species of humpback dolphins. Specimens examined and referred are provided in Appendix S2. The four proposed species are described below:

*SOUSA TEUSZII* (KÜKENTHAL, 1892)

*Synonymy*

- Sotalia teuszii* Kükenenthal, 1892: 442, pl. 21. Basionym  
*Sotalia Teuszii* Van Beneden, 1892: 351. Alternate spelling.  
*Sotalia teuszi* Hershkovitz, 1966: 25. Alternate spelling.

*Holotype and Type Locality*

The holotype is a skull previously thought to be in the Jena Natural History Museum, but now known to be housed in the Natural History Museum, London (BMNH 1893.8.11). Type locality is “Bucht des Kameruner Kriegsschiffhafens” (the Bay of Warships, Cameroon, West Africa; Hershkovitz 1966). The skull was not figured by Kükenenthal (1892), but was illustrated in van Beneden (1892) and Pilleri and Gahr (1972). Best (2007) illustrated the skull from another specimen.

*Diagnosis*

*Sousa teuszii* reaches a known maximum total length of 266 cm (less than the other species), though the sample of measured individuals is small (Fig. 5). The species is characterized by a prominent dorsal hump in all individuals (though less exaggerated in calves), ranging from 26% to 32% of body length (Ross *et al.* 1996), and a small dorsal fin with a more-rounded dorsal fin tip than *S. plumbea* (Fig. 8; see photographs in Weir 2011). Based on a very small sample ( $n = 2$ ), this species appears to have more vertebrae on average (52–53 *vs.* as few as 49–50) than other species of *Sousa*. The length/breadth ratio of the cranium is 2.1–2.4. The rostrum of *S. teuszii* is relatively shorter than in the other species of humpback dolphins (in skull measurements reaching a known maximum of 308 mm, *vs.* at least 339 mm in the other species). Tooth counts are lower than in other *Sousa* species (27–32 *vs.* 31–39). The color pattern is a uniform dark gray, with only slight spotting, if any. There are no shared mtDNA haplotypes with other species, and a compound diagnostic mtDNA character that distinguishes *Sousa teuszii* from other *Sousa* species; nuDNA characters diagnose *S. teuszii* + *S. plumbea* from all other *Sousa* (Table 2).

*Coloration*

Most individuals have a relatively-uniform dark gray pattern with a lighter ventral surface. The upper parts appear more grayish than in *S. plumbea*, which can have a



Figure 8. The external appearance of *Sousa teuszii*: lateral view (upper), close-up of dorsal fin (middle), and close-up view of head (lower) of specimens from entanglements in Gabon and the Congo. Upper and lower views of a 250 cm female, and middle view of a 266 cm male. Photographs by T. Collins.

brownish hue. Some larger adults have a white margin to the dorsal hump and fin, apparently caused by scarring, and there may be some white or dark flecking on the tail stock (Weir 2011). Color pattern differences between this species and *S. plumbea* have not been systematically studied, and any real differences between the species may have been masked by developmental and sexual variation. There is a faint delphinid bridle (Perrin 1997).

#### *Osteology*

As detailed in Table 1, the skull of *S. teuszii* has a relatively short rostrum, the length-breadth ratio of the skull is lower than in other humpback dolphin species, and both upper and lower average tooth counts are much lower (Ross *et al.* 1996,

Jefferson and Van Waerebeek 2004). Based on a small sample, Pilleri and Gihl (1972) reported 52–53 vertebrae for two specimens of *S. teuszii* (data from Cadenat 1956, Cadenat and Paraiso 1957), more than for *S. plumbea* (Fig. 4).

### *Geographic Variation*

No subspecies are recognized, and there is no convincing evidence of geographic forms or clines throughout the range of the species. Eight management stocks have been recognized, but these are largely based on apparent distributional gaps, at least some of which may be secondarily caused by human impacts (Van Waerebeek *et al.* 2004), but also may represent no or low survey effort.

### *Distribution*

This species is found in the shallow coastal waters of western African from Dahkla Bay, Western Sahara (23°50'N) to Tombua, Angola (15°47'S) (Fig. 9). Distribution appears to be discontinuous, with some evidence of separate populations/metapopulations (Van Waerebeek *et al.* 2004, International Whaling Commission 2011). Currently-known range states include Western Sahara, Mauritania, Senegal, The Gambia, Guinea Bissau, Guinea, Cameroon, Gabon, Republic of the Congo, and Angola (Weir 2011), but the distribution of *S. teuszii* is thought to contain most countries in between. Waters of Ghana may represent a gap in distribution, and whether it occurs today in Nigeria is unknown (International Whaling Commission 2011). Van Waerebeek *et al.* (2004) suggested *S. teuszii* most likely inhabited the Niger Delta before the large-scale oil exploration and extraction altered the coastal environment.

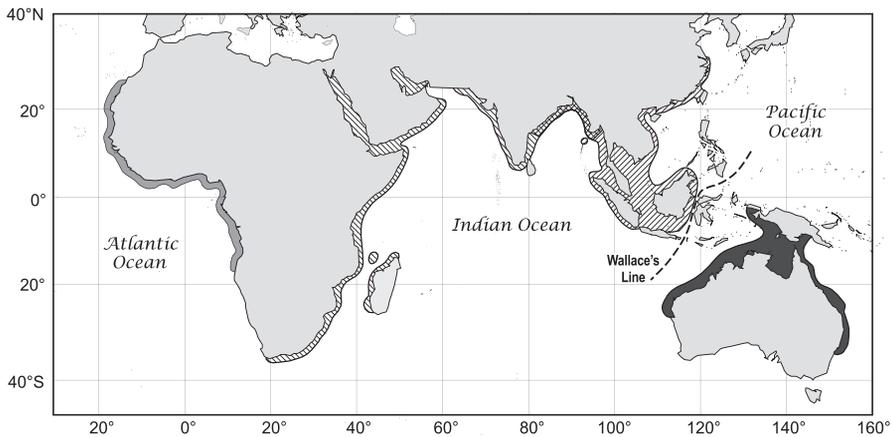


Figure 9. Suggested ranges of the different species of *Sousa*: *S. teuszii* (light shading), *S. plumbea* (135° hatching), *S. chinensis* (45° hatching), and *Sousa sabulensis* sp. nov. (dark shading). The gaps shown are all believed to be real, based on lack of records, but not all waters of eastern Indonesia have been extensively surveyed for cetaceans.

### *Habitat/Ecology*

The habitat of the species consists mostly of shallow coastal marine and estuarine waters with soft-sediment bottoms (Weir 2011). There is no convincing evidence that they ascend rivers beyond the influence of marine waters (Van Waerebeek *et al.* 2004). There is currently no good evidence of significant seasonal movements in this species, and in at least one place (Angola) where detailed ecological studies have been conducted, the population appears to be very small (10 individuals), resident, and undoubtedly threatened by human activities (Weir 2011).

### *Life History*

Life history data are almost nonexistent for this species. There is very little information available on the size of this species, as only 20 specimens appear to have been measured. Reported lengths were 107–266 cm, and 14 specimens  $\geq 200$  cm averaged  $240.4 \pm \text{SD } 16.46$  cm. Six males  $\geq 200$  cm averaged 237.2 cm long, and three females were 226, 235, and 250 cm long. The sample is too small to determine if significant sexual dimorphism exists, but based on the related *S. plumbea*, we suspect that males grow larger than females.

### *Etymology*

The species is named in honor of Edward Teusz, who collected the specimen that later became the type and donated it to Dr. Kükenthal at the Jena Natural History Museum. The English common name is the currently used Atlantic humpback dolphin.

### *Conservation Status*

*Sousa teuszii* is listed as Vulnerable on the IUCN Red List (Reeves *et al.* 2011). No range wide estimate of overall abundance exists, but the species is thought to be at risk and potentially declining throughout its range (Van Waerebeek *et al.* 2004, International Whaling Commission 2011, Weir *et al.* 2011). Total abundance of the species probably numbers no more than a few thousand individuals (see Weir *et al.* 2011). Van Waerebeek *et al.* (2004) recognized eight provisional management stocks, based on the fragmentary information available at the time. One of the smallest stocks appears to be that in Dahkla Bay, Western Sahara, which may number only in the low tens of individuals (Van Waerebeek *et al.* 2004). An even-smaller, resident group of only about 10 individuals occurs in the Flamingos area of Angola (Weir 2011). The largest/healthiest stock known is that in the Arquipelago dos Bijagos, Guinea Bissau, which although detailed ecological studies have not been conducted, appears to number at least several hundred individuals (Van Waerebeek *et al.* 2004). There are apparent regional pockets of relatively high density, such as Senegal/Gambia, Guinea Bissau/Guinea/Sierra Leone, Gabon/Congo, and Cameroon/Angola (International Whaling Commission 2011). Although many threats face the species throughout its range, bycatch in coastal fisheries appears to be the greatest immediate threat to most populations (Weir *et al.* 2011). Other threats include direct hunting (including for “bushmeat”), habitat loss and degradation, prey depletion (often caused by overfishing), environmental contamination, coastal development, oil and gas exploration and development, anthropogenic noise, and habitat alteration from eutrophication and

climate change (see International Whaling Commission 2011, Weir 2011, Weir *et al.* 2011). A series of recommendations for conservation and research was recently made by the International Whaling Commission (2011).

*SOUSA PLUMBEA* (G. CUVIER, 1829)

#### *Synonymy*

- Delphinus plumbeus* G. Cuvier, 1829: 288. Basionym.  
*Delphinus (Steno) lentiginosus* Owen, 1866: 20, pl. V, figs. 2 and 3. Junior synonym.  
*Steno (Sousa) lentiginosus* Gray, 1866a: 213. New name combination.  
*Sotalia plumbeus* Flower, 1883: 489, 513. New name combination.  
*Sotalia lentiginosus* Flower, 1883: 489, 513. New name combination.  
*Steno plumbeus* Blanford, 1888: 583. New name combination.  
*Sotalia plumbea* True, 1889: 21, 153. Alternate spelling.  
*Steno lentiginosus* Blanford, 1891: 584. New name combination.  
*Sotalia fergusonii* Lydekker, 1903: 411, pl. D. Junior synonym.  
*Sousa lentiginosa* Iredale and Troughton, 1934: 68. New name combination.  
*Stenopontistes zambezius* Miranda-Ribiero, 1936: 20. Junior synonym.  
*Sotalia lentiginosa* Deraniyagala, 1945: 119. Alternate spelling.  
*Sousa plumbea* Fraser and Purves, 1960: 60. New name combination.

#### *Holotype and Type Locality*

The holotype is a skull in the Muséum national d'Histoire naturelle, Paris as MNHN A-3053, but is also labeled with A-14378. Type locality is "Malabar," northern Kerala, in southwestern India. The holotype skull is illustrated by drawings in van Beneden and Gervais (1880, plate XXXVII, fig. 1–5), and just the lateral view is reprinted in True (1889, plate 1, fig. 2). The holotype and syntypes are described in detail in Robineau (1990).

#### *Diagnosis*

This is the largest species of humpback dolphin, reaching reliably reported maximum total lengths of 279 cm (Cockcroft 1989; Fig. 5). Specimens of *S. plumbea* have a prominent dorsal hump in adult-size age classes, and the hump is even visible (though less pronounced) in young animals (Fig. 10). The hump ranges in length from 23% to 38% of body length (Ross 1984, Best 2007), and is most exaggerated in adult males (Cockcroft 1989). In general, the dorsal fin is small and the tip is more pointed and falcate than it is in *S. teuszii* (Fig. 10). There are 49–52 total vertebrae, and the typical vertebral formula is C7, Th11–12, Lu9–13, Ca18–23. The rostrum is relatively long (up to 377 mm). The length/breadth ratio of the cranium is 2.2–2.8. Tooth counts are relatively high (33–39 *vs.* as low as 27 for the other species). Coloration is a uniform brownish-gray, with a lighter belly and only slight if any spotting. There are no shared mtDNA haplotypes with other species, and two diagnostic mtDNA characters that distinguish *Sousa plumbea* from other *Sousa* species. Additionally, nuDNA characters diagnose *S. teuszii* + *S. plumbea* from all other *Sousa* (Table 2).



Figure 10. The external appearance of *Sousa plumbea*: mother and calf caught in a shark net in South African waters (upper), and close-up of the head of the adult (lower). Note that even the calf has a prominent dorsal hump. Lengths unknown. Photographs by the Natal Sharks Board.

#### Coloration

Coloration of most individuals is a relatively uniform brownish-gray pattern with a lighter belly, although white scarring and dark flecking/speckling is often present in larger individuals, especially on the dorsal fin/hump and tail stock (Best 2007). Dolphins from southern Africa are somewhat lighter ventrally than those from Tanzania/Kenya or the Arabian region, which appear more brownish on the dorsal surface (and much more so than *S. teuszii*, which is more of a dark gray). Most larger adults have a white margin to the dorsal hump and fin, apparently caused by scarring (see Jefferson and Karczmarski 2001). Color pattern differences between this species and *S. teuszii* have not been systematically studied, and any differences may have been masked by the significant amount of developmental and sexual variation. There is a faint delphinid bridle (Perrin 1997).

#### Osteology

In the skull of this species, the rostrum is relatively long, and the length/breadth ratio of the cranium (as measured by condylobasal length/zygomatic width) is on average larger than in other species of humpback dolphins. Average tooth counts are also higher than in other species of the genus (see Jefferson and Van Waerebeek 2004). Vertebral counts range from 49 to 52, with a typical formula of C7, Th11–12, L10–14, and Ca18–23 (Lydekker 1903, Pilleri 1971, Robineau and Rose 1984,

Ross 1984). Deraniyagala (1945) reported on a specimen with 69 vertebrae from Sri Lanka, but this is undoubtedly an error.

### *Geographic Variation*

This species is highly variable, and there is some evidence for the existence of several geographic forms (see Ross *et al.* 1996), which could receive subspecies consideration after additional data are collected. Within the western Indian Ocean, Mendez *et al.* (2011) found evidence of significant genetic structure suggesting separate populations in three regions: (1) South Africa/Mozambique, (2) Tanzania, and (3) Oman. Dolphins along the East African coast appear to be distinct from those along the coastline of Oman and the Indian subcontinent. The East African form appears to have a gray ground color pattern. If eventually recognized as a subspecies, the available nominal name is *zambezius* (Miranda-Ribiero 1936).

Humpback dolphins further east, from at least parts of western India to Sri Lanka, appear to have a white ground color, and the adults appear to be heavily covered with dark flecking (see Ross *et al.* 1996). Photographs show that in many of these animals, much of the back and upper sides are dark, but that the belly, lower sides, and the sides of head are light with sometimes extensive dark flecking. This form was first described as *Delphinus (Steno?) lentiginosa* by Owen (1866) (Fig. 11). The type location is Waltair, Vizagapatam, Madras Bay, India. After more data are collected on this nominal species it may be found to be a distinct subspecies. Although in many ways it appears intermediate between *S. plumbea* and *S. chinensis*, current molecular evidence does not suggest that it is a hybrid/intergrade. Additional work needs to be done to determine if there are reliable morphological and/or coloration differences that can be used to distinguish these putative subspecies, so no trinomials are proposed for recognition at this time.

There is also some evidence to suggest that there might be a dwarf form of this species occurring in the Persian Gulf (see Jefferson and Van Waerebeek 2004), and future research on this form could eventually show it to represent yet another subspecies. Obviously, much more work needs to be done on the smaller-scale variation in the *plumbea* species to determine whether any of these or other geographic forms deserves subspecies status.

### *Distribution*

This species is found in shallow waters from Muizenberg, False Bay, South Africa (Best 2007) to the Bay of Bengal, as far east as the Mergui Archipelago, southeastern Myanmar (Burma), including the Red Sea and Persian (Arabian) Gulf (Jefferson and Karczmarski 2001, Smith and Tun 2008) (Fig. 9). Occasional records of *Sousa* from as far north as Saldanha Bay have been recently reported from Southwest Africa.<sup>2</sup> Range states with confirmed records include South Africa, Mozambique, Madagascar, the Comoros, Kenya, Tanzania, Somalia, Ethiopia, Oman, United Arab Emirates, Saudi Arabia, Djibouti, Bahrain, Egypt, Iran, Iraq, Kuwait, Qatar, Yemen, Pakistan, India, Sri Lanka, Bangladesh, and Myanmar (Burma). There is an extralimital record from Israel, where one individual recently passed through the Suez Canal into the Mediterranean Sea (Kerem *et al.* 2001).



Figure 11. The *lentiginosa* form of *S. plumbea*, which has extensive spotting and flecking on the body in adults. It is not yet apparent whether this is a distinct geographic form, or whether this color pattern may be associated with particular age/sex classes. Length unknown. Specimen from Sri Lanka, photograph by R. Nanayakkara.

#### *Habitat/Ecology*

Populations of *S. plumbea* are found in shallow, nearshore waters, most often in a narrow strip along the coast, with apparently higher densities around estuaries (Ross *et al.* 1994, Jefferson and Karczmarski 2001). They rarely occur in waters deeper than about 30 m. Some seasonality of movements has been noted in certain areas, but in general the animals show limited movements and residency is common in many parts of the range (see Jefferson and Karczmarski 2001, Guissamulo and Cockcroft 2004). However, long distance movements on the order of several hundred linear kilometers are known (Keith *et al.* 2002). Most populations that have been studied using photo-identification techniques apparently have a fission/fusion society, with only short-term association patterns beyond that of the mother and calf (see Jefferson and Karczmarski 2001).

#### *Life History*

Reliably reported total lengths were 87–279 cm ( $n = 235$ ), and 152 specimens  $\geq 200$  cm averaged  $227.7 \pm \text{SD } 19.88$  cm. Two exceptionally large specimens have been reported from India, an adult male of 320 cm (reported as 10'6"; Sterndale 1887, Blanford 1888), and a male in the range category of 325–350 cm (Lal Mohan 1985). Although Indian specimens do appear to grow very large (based on cranial lengths), we consider the above reported total lengths implausible, and do not think lengths over about 290 cm are reached. This species is sexually dimorphic. Males  $\geq 200$  cm averaged  $230.9 \pm \text{SD } 22.85$  cm (range = 200–279 cm,  $n = 74$ ), but females averaged only  $224.0 \pm 16.00$  cm (range = 200–263 cm,  $n = 60$ ). Based on a large sample, South African humpback dolphins are born at 100 cm and reach lengths up to 279 cm and weights of 260 kg, with males achieving an asymptotic length of 270 cm, but females only 240 cm (Cockcroft 1989). Lengths of 88 specimens from the Arabian Gulf ranged from 93 cm to 269 cm (Ross *et al.* 1996). Specimens from India (and Pakistan) appear to be exceptionally large, based on skull lengths and scanty total length data from the literature (Jefferson and Van Waerebeek 2004). Although there is very little total length information available from India, Lal Mohan (1985) reported one animal over 325 cm, and Sterndale's (1887) specimen was measured at 320 cm. Life history of this species has only been studied in detail in South Africa,

where specimens have been collected from strandings and animals bycaught in shark nets set around beaches to protect bathers (Cockcroft 1989). In South Africa, peak calving occurred in summer months, and the average calving interval was 3 yr. Length at birth was estimated at 100 cm, female sexual maturity was attained at 10 yr and male maturity at 12–13 yr. Asymptotic length was reached at an estimated 240 cm for females and 270 cm for males, and maximum weight was around 260 kg. Dolphins in this population live to ages of over 40 yr (Cockcroft 1989), and Cockcroft (in Best 2007) suggested that longevity in both sexes could reach over 46 yr.

#### *Etymology*

The species name, *plumbea*, refers to the dark gray (plumbeous, or lead-colored) color of the body. The English common name is the Indian Ocean humpback dolphin, which accurately describes its range.

#### *Conservation Status*

Currently, the IUCN Red List includes an assessment for only a single species of *Sousa* in the entire Indo-Pacific region (as *Sousa chinensis*), and the range-wide status is evaluated as Near Threatened. However, recognizing their probable taxonomic distinctness, the account includes separate discussions for *Sousa chinensis* and *S. plumbea*, and if they were assessed separately, *S. plumbea* would be evaluated as Vulnerable (Reeves *et al.* 2011). No overall estimates of abundance throughout the range exist, but available estimates for specific populations suggest that the range-wide abundance is probably no higher than the low tens of thousands. Available estimates of abundance for particular areas include 450 individuals in Algoa Bay, South Africa (Karczmarski 1996), 170–244 individuals in Richards Bay, South Africa (Atkins and Atkins 2002), 105 in Maputo Bay, Mozambique (Guissamulo and Cockcroft 2004), *ca.* 60 in the Bazaruto Archipelago, Mozambique (Guissamulo and Cockcroft 1997), and 58–65 off Zanzibar, eastern Africa (Stensland *et al.* 2006). Although detailed studies have only recently been done, preliminary indications are that population(s) in Sri Lanka may be small and near extirpation, with only a few tens of individuals remaining (Broker and Ilangakoon 2008). There are suggestions of declines in abundance of some populations of *S. plumbea*, but for the most part population trends have not been systematically studied in this species (Cockcroft 1990, Durham 1994, Reeves *et al.* 2011). Major threats to the species throughout most or all of its range include fisheries and shark-net bycatch, as well as habitat loss and degradation. Other threats that appear somewhat less serious or only affecting certain portions of the range include direct killing, environmental pollution, boat traffic/harassment, and oil spills (the latter especially in the Persian/Arabian Gulf area) (Ross *et al.* 1994, Jefferson and Karczmarski 2001, Best 2007, Reeves *et al.* 2011).

*SOUSA CHINENSIS* (OSBECK, 1765)

#### *Synonymy*

*Delphinus chinensis* Osbeck, 1765: 7. Basionym.

*Delphinus sinensis* Desmarest, 1820: 514. Alternate spelling.

*Steno chinensis* Gray, 1871: 65. New name combination.

*Sotalia sinensis* Flower, 1883: 488. New name combination.

*Sotalia borneensis* Lydekker, 1901: 88. Junior synonym.

*Sotalia chinensis* Allen, 1938: 499. Alternate spelling.  
*Sousa borneensis* Fraser and Purves, 1960: pl. 25. New name combination.  
*Sousa huangi* Wang, 1999: 309. Junior synonym.

#### *Holotype and Type Locality*

Type locality is the “Canton River” (= Pearl River, People’s Republic of China). There is no holotype, but a specimen was described and beautifully illustrated by Flower (1870). This individual was viewed as a kind of surrogate for a type specimen until its destruction in the Museum of the Royal College of Surgeons during a bombing raid in World War II (Pilleri 1979). Porter (2002) recently designated a neotype for *Sousa chinensis* (BMNH ZD 1999.360), but the male individual was only 5 yr of age, well below the age at which males reach sexual maturity, which is about 12–14 yr, and physical maturity—about 14–17 yr (see Jefferson *et al.* 2012). Therefore, as suggested by Jefferson and Van Waerebeek (2004), Porter’s (2002) neotype may not have the characteristics typical of adults of the species, and on which taxonomic comparisons are usually made. Also, several errors were made in the description. Therefore,

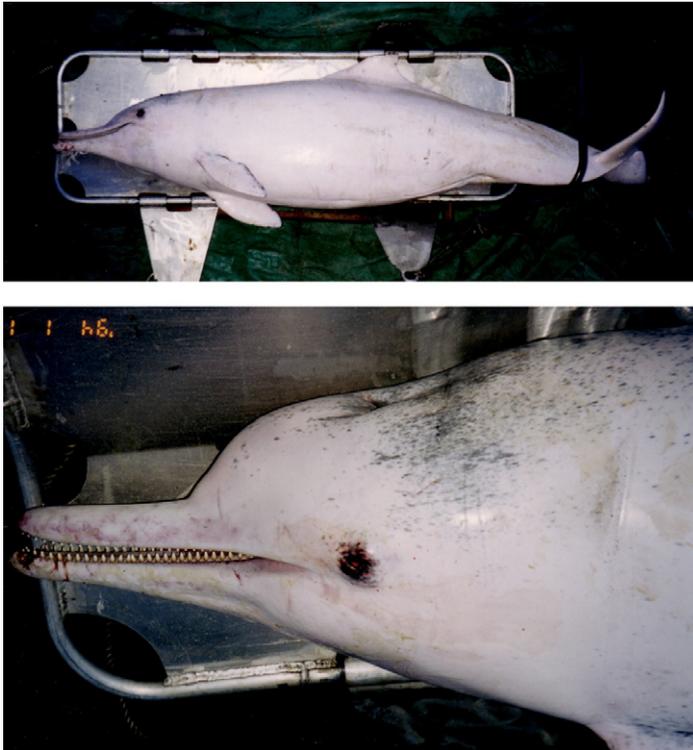


Figure 12. The external appearance of *Sousa chinensis*: lateral view (upper), and close-up of head (lower) of a 235 cm young adult female stranded in Hong Kong waters. Photographs by D. Choi, Agriculture, Fisheries and Conservation Department, Hong Kong SAR Government.

we emphasize that Porter's (2002) neotype description should not be used for comparative purposes without due consideration to these problems.

### *Diagnosis*

*Sousa chinensis* reaches a known maximum total length of 270 cm (Fig. 5). The species is characterized by the absence of a dorsal hump, and a low, wide-based (ranging from 15%–21% of body length; Zhou *et al.* 1980; TAJ, unpublished), triangular to slightly-falcate dorsal fin (Fig. 12; Jefferson and Karczmarski 2001). There are 50–53 total vertebrae, and the typical vertebral formula is C7, Th12–14, L9–11, Ca21–24. The rostrum is relatively short (to 339 mm). The length/breadth ratio of the cranium is 2.2–2.6. Tooth counts are between those of other *Sousa* species (32–38 per tooth row). Adults are mostly white, but with some dark spotting and/or gray patches in some populations (there is no cape pattern). There are no shared mtDNA haplotypes with other species, and three diagnostic mtDNA characters that distinguish *Sousa plumbea* from other *Sousa* species. A single nuDNA character diagnoses *S. chinensis* from all other *Sousa* (Table 2).

### *Coloration*

Although newborns are gray in color, adults of this species have much more extensive white coloration on the body than in other species of *Sousa*, and in at least some parts of the range (*e.g.*, Chinese waters) most adults are completely white, although often with small dark spots on the back and/or dorsal fin (Jefferson and Karczmarski 2001, Wang *et al.* 2008). In Chinese waters, older females may become pure white, though males appear to retain more dark spotting on the body into old age (Jefferson *et al.* 2012). Although juveniles may show evidence of a faint delphinid bridle, there is no trace of it in adults, at least in populations around the South China Sea (Perrin 1997).

### *Osteology*

In the skull, the rostrum is relatively short, and the length/breadth ratio of the cranium is intermediate between *S. teuszii* and *S. plumbea*. The skull is generally shorter on average than in *S. plumbea* and tooth counts are slightly lower (Jefferson and Van Waerebeek 2004). Vertebral counts range from 50–53, with a typical formula of C7, Th12–14, L9–11, and Ca21–24 (Flower 1870, Wang and Sun 1982, Zhou *et al.* 1997, Liu *et al.* 1999, Wang 1999, Zhou *et al.* 2007). Porter (2002) reported a vertebral formula for her proposed neotype of C7, Th12, L23, and Ca18 (total 60), which is certainly erroneous. In an earlier paper (Porter 1998), she gave the same formula in the text, but in a table listed the formula for that specimen as C7, Th12, L12, and Ca18 (total 49). Although the count from Porter (1998) appears more reasonable, these errors and inconsistencies further support our suggestion that the neotype specimen proposed by Porter (2002) should not be used in taxonomic comparisons.

### *Geographic Variation*

There is some evidence for the existence of several geographic forms of this species. Animals from the coast of China/Taiwan are white as adults, with some spotting on at least younger animals – older adult females are often pure white (see Jefferson *et al.*

2012). This geographic form is described in detail, including differences in external appearance of various age and sex classes, by Jefferson *et al.* (2012), and it may eventually be recognized as the subspecies *Sousa chinensis chinensis* (Osbeck, 1765). The Taiwanese white dolphin (a distinct population found in the Eastern Taiwan Strait) has some color pattern differences from populations along the mainland coast of China (Wang *et al.* 2008). There may be more than one form that deserves subspecific status in this region. At any rate, there are clearly several populations of *Sousa chinensis* along the Chinese coastline, which should be managed as separate stocks (Jefferson 2000, Wang *et al.* 2008, Chen *et al.* 2010).

Although little-studied, humpback dolphins south of China, throughout Southeast Asia appear to have more extensive dark coloration as adults and apparently even lower and wider-based dorsal fins. These have been called the *borneensis* form, because they are similar to the nominal species *Sotalia borneensis* described by Lydekker (1901) from Sarawak. However, it is unclear where the distributional break occurs, or even if there is a distinct break or perhaps clinal variation. Lin *et al.* (2010) suggested that there are at least two different sublineages in Southeast Asia, and our review provisionally supports this hypothesis. There is some suggestion of further variation within animals from Southeast Asia, but this is not well documented, as very few specimens of these animals have been examined, and the issue needs further study to determine if there is indeed significant geographic variation. No trinomials are proposed for recognition until such further study is conducted.

### *Distribution*

This species is distributed in waters from central China (near the mouth of the Yangtze River), south throughout the waters of Southeast Asia as far southeast at least as Borneo, and as far west as the Orissa coast of India (Sutaria and Jefferson 2004) (Fig. 9). It overlaps in range with *Sousa plumbea*, although there is no convincing evidence of interbreeding between the two species (see above). Range states include the People's Republic of China (including the SARs of Hong Kong and Macau), Taiwan (Republic of China), Vietnam, Cambodia, Thailand, Myanmar (Burma), Bangladesh, India, Indonesia, Malaysia, Singapore, and Brunei Darussalam.

### *Habitat/Ecology*

A very large portion of what is known of this species' ecology comes from extensive, long-term studies conducted in Hong Kong and surrounding waters, although in recent years detailed studies have also been conducted in Taiwan and also along some areas of the mainland coast of China, with similar results. The habitat of the species consists of shallow, coastal marine waters and especially waters in and around large estuaries (Jefferson and Karczmarski 2001). Within Hong Kong, they prefer deeper-water channels for feeding, and appear in higher densities along natural rocky coastlines that may harbor good feeding opportunities (Hung 2008). They appear to occur anywhere where there is a riverine influence, but do not occur in the strictly-marine waters of Hong Kong (Jefferson 2000, Hung 2008). Their social organization is one of a fission/fusion society, with two partially-sympatric communities, and mostly short-term associations (Jefferson 2000, Dungan 2011), and their ranging/movements tend to be over relatively small areas from 39 to 339 km<sup>2</sup>, and averaging 135 km<sup>2</sup> (Hung 2008). Interestingly though, the much-smaller population off the west coast of Taiwan

has a very different social pattern, being much more homogeneous and with long-lasting associations being the rule (Dungan 2011). This may be the product of the very different environments (linear ranges in Taiwan and convoluted in Hong Kong) and population sizes (<100 in Taiwan and >2,000 in Hong Kong/Pearl River Estuary) of the two populations.

### *Life History*

The biology of this species has only been studied in detail around Hong Kong and the Pearl River Estuary of China, where specimens have been collected mostly from strandings and thus decomposition affected the sample (Jefferson *et al.* 2012). Peak calving occurred in spring to early summer months (March to June), and the average calving interval was 5 yr. Length at birth was estimated at 101 cm, female sexual maturity was attained at about 9–10 yr and male maturity at 12–14 yr (but the latter based on very small sample sizes). Asymptotic length was reached at an estimated 249 cm for both sexes, age at physical maturity was around 14–17 yr, and maximum weight was around 240 kg. Based on tooth aging, dolphins in this population live to ages of over 38 yr (Jefferson *et al.* 2012). Most external morphometric information for this species comes from China. Reported lengths were 89–270 cm ( $n = 162$ ), and 92 specimens >200 cm averaged  $236.9 \pm \text{SD } 15.20$  cm. Males >200 cm averaged  $235.5 \pm \text{SD } 16.88$  cm (range = 205–270 cm,  $n = 6$ ), and females averaged  $237.8 \pm 9.66$  cm (range = 216–254 cm,  $n = 33$ ). There appears to be little or no sexual dimorphism in body length and shape in this species in general.

### *Etymology*

The species name, *chinensis*, refers to the original location of the animals observed by Osbeck, in the Canton (Pearl) River of southern China. We considered the Western Pacific humpback dolphin, but this is not accurate, as the species occurs in both the Indian and Pacific oceans. The suggested common name is therefore the currently used Indo-Pacific humpback dolphin, which accurately describes its range.

### *Conservation Status*

Currently, the IUCN Red List includes an assessment for only a single species of *Sousa* in the Indo-Pacific (*S. chinensis*) covering this and the species outlined above, and the taxon is listed as Near Threatened. However, recognizing their probable taxonomic distinctness, the account includes separate discussions for *Sousa chinensis* and *S. plumbea*, and if they were assessed separately, *S. chinensis* would be evaluated as Vulnerable (Reeves *et al.* 2011). There are no global abundance estimates that apply to this species, but based on estimates from where surveys have been done, there would appear to be several thousand to possibly up to about 10,000 throughout the range. There are five populations that have been assessed with sighting surveys, all from the coasts of China: (1) Eastern Taiwan Strait (99 individuals; Wang *et al.* 2007), (2) Xiamen/Jiulong River Estuary (ca. 86 individuals; Chen *et al.* 2008), (3) Hong Kong/Pearl River Estuary (2,555 individuals; Chen *et al.* 2010), (4) Leizhou Peninsula (237 individuals; Zhou *et al.* 2007), and (5) Sanniang Bay, Beibuwan Gulf (>98 individuals; Pan *et al.* 2006). Although for most populations, there is no information on trends in abundance, there are strong suspicions of declines in several (*e.g.*, Taiwan and Xiamen; Jefferson and Hung 2004, Wang *et al.* 2007). In Hong Kong, dolphin

numbers are declining, but it is unknown if this is a result of an overall population decline or simply shifts of animals into other areas outside Hong Kong's boundary, because the area inhabited in Hong Kong is a small part (<5%) of the whole Pearl River Estuary range (TAJ, unpublished). Overall, it seems likely that the species may be in decline, due to the extensive degradation of coastal habitat that has occurred throughout so many parts of their range. Major threats to the species include fisheries bycatch, vessel collisions, environmental contamination, and habitat loss and degradation. Threats seen as less critical include occasional direct kills, noise disturbance, prey depletion from overfishing, and disturbance from ecotourism activities. There is active management of this species in Hong Kong (see Jefferson *et al.* 2009), and to a much lesser extent in Taiwan and Mainland China.

*SOUSA SAHULENSIS* SP. NOV.

#### Synonymy

*Sousa queenslandensis* Gaskin, 1972: 124, fig. 101. *Nomen nudum*.

#### Holotype and Type Locality

The holotype is a complete skull in the Museum of Tropical Queensland (MTQ JM20036), collected on 23 June 1985 from Saunders Beach, northeast Queensland,

Table 3. Cranial measurements (in mm) for the type specimen of *S. sabulensis* (MTQ JM20036) and means for the species.

Measurement	MM 1019	Mean
Upper tooth count	31	33.0
Lower tooth count	33	32.8
Tooth diameter	7.2	6.60
Condylbasal length	507	507.9
Length of rostrum	308	308.6
Width of rostrum at base	106	109.1
Width of rostrum at 1/2 length	47	46.6
Width of rostrum at 3/4 length	31	32.9
Width of premax. at 1/2 length	30	31.0
Greatest width of premax.	78	76.7
Preorbital width	187	184.6
Postorbital width	217	210.8
Zygomatic width	219	211.7
Parietal width	136	145.6
Width of external nares	50	50.6
Width of internal nares	60	61.2
Length of temporal fossa	113	108.5
Height of temporal fossa	97	90.4
Length of orbit	57	56.5
Length of antorbital process	38	40.0
Length of upper tooth row	268	270.5
Length of mandible	432	434.9
Height of mandible	86	85.5
Length of mandibular symphysis	129	129.2
Length/breadth ratio	2.3	2.39

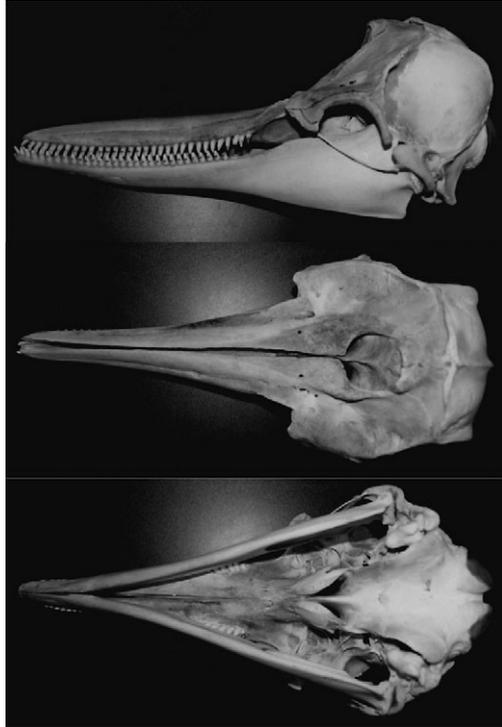


Figure 13. The holotype specimen of *Sousa sabulensis* sp. nov., a skull in the Museum of Tropical Queensland (MTQ JM20036). The specimen (CBL = 507 mm) was collected from Saunders Beach, NE Queensland, Australia: lateral view (upper), dorsal view (middle), and ventral view (lower).

Australia ( $19^{\circ}09'20''S$ ,  $146^{\circ}36'26''E$ ). The skull is from an adult male specimen 227 cm in total length (CBL = 507 mm), and was measured by TAJ in June 2000 (measurements presented in Table 3). The skull of the holotype is illustrated in Figure 13. A bone sample from the type specimen has been obtained for genetic analysis and the mtDNA control region sequence will be deposited in GenBank. No paratypes are proposed.

#### *Diagnosis*

*Sousa sabulensis* is known to reach total lengths of up to 270 cm (Fig. 5). In this species, there is no visible dorsal hump and the dorsal fin is low and triangular, with a wide base ranging from 14% to 24% of body length (Ross *et al.* 1996; Fig. 6). Vertebral counts based on only two specimens (both with 50 total vertebrae) suggest that vertebral counts may be lower than in other species. The length/breadth ratio of the cranium is 2.2–2.5. The rostrum is relatively short (to 350 mm), and tooth counts are moderately low (31–35 per tooth row). The color pattern is very different than in the other species in the genus, with adults having a dark gray back and lighter belly separated by an indistinct curved “cape” margin. White blotches and spotting are common. There are no shared mtDNA haplotypes with other

species, and seven diagnostic mtDNA characters that distinguish *Sousa sabulensis* from other *Sousa* species. A single nuDNA character diagnoses *S. sabulensis* from all other *Sousa* (Table 2).

### *Coloration*

While there appears to be extensive intraspecific variation in the color pattern, which has not yet been adequately documented, in general, Australian humpback dolphin adults are gray in color, with variable amounts of white scarring and dark flecking on the head, back, dorsal fin, and tail stock. Photographs of animals from Papua New Guinea do not show any obvious differences in coloration. In *S. sabulensis*, most large adults are primarily dark gray with a lighter belly and lower sides, and the separation of the dark back and lighter ventrum is bounded by a slightly curved, diagonal “cape” line with indistinct margins, and often invaded by an oval area of light color from below (see Fig. 6). This cape feature is not present in any other species of humpback dolphin. Although older adults may have large unpigmented areas, including much of the head, they do not appear to become completely white (as at least some specimens of *S. chinensis* do). “Amity” (a captive specimen of *S. sabulensis* estimated at 48 yr of age) still has large patches of dark color on her back and sides. Young calves are somewhat darker than the adults. There is some evidence of a blow-hole stripe, but any evidence of an eye stripe appears to be faint at best.

### *Osteology*

The skull is similar in appearance to that of *S. chinensis*, but tooth counts are significantly lower on average than in any other species of *Sousa*, with the exception of *S. teuszii* (see Jefferson and Van Waerebeek 2004; Fig. 2, 3). There is no detailed description of the skeleton and few vertebral count data available for *S. sabulensis*.

### *Geographic Variation*

Lin *et al.* (2010) suggested that humpback dolphins in eastern and western Australia may have been separated by the Torres Strait land bridge when sea levels were lower than today. The current depth of the Torres Strait is only about 12 m, and from 7,000–115,000 yr ago sea level was below this level, forming a land bridge (Blair *et al.* 2014). The separation of humpback dolphins on east and west sides of this land bridge might have resulted in different geographic forms that could persist today, as is the case with the dugong (*Dugong dugon*; Blair *et al.* 2014). Samples used by Lin *et al.* (2010) from eastern and western Australia showed some differences in haplotype frequency, but sample sizes were small. There is currently no solid evidence for the existence of geographic forms in this species, although this appears likely and it might be expected that animals from New Guinea might have evolved some differences from those in Australia as well. Australian humpback dolphins do occur in more-or-less discrete populations where they have so far been studied (Parra *et al.* 2004).

### *Distribution*

This species is found in the tropical/subtropical waters along the coast of northern Australia, from the Queensland/New South Wales border (31°27'S) to Ningaloo Reef, near Exmouth Bay (22°17'S; Parra *et al.* 2004; Fig. 9). There are seven reliable

records (supported by photographs) of humpback dolphins reported from near Kikori, Gulf of Papua, in southern Papua New Guinea in 2013.<sup>3</sup> An additional two unconfirmed records have been reported from the same area.<sup>4</sup> Therefore, humpback dolphins (apparently *S. sabulensis*) also occur in at least the southern waters of the island of New Guinea (as was suggested by Mitchell 1975 following Dawbin 1972, but with no details given). Generally, there is very little information available on marine mammal distribution in waters of far-eastern Indonesia and Papua New Guinea. There are reports of humpback dolphins (species unknown) from Bintuni-Berau Bay, West Papua/Irian Jaya, Indonesia (B. Kahn, *in litt.*, 2006); however these must be considered unconfirmed, as detailed descriptions or photographs were not provided. Based on its apparent distribution, *Sousa sabulensis* is considered to be associated with the Sahul Shelf, which extends around Australia and connects to southern New Guinea. Known range states to date include Australia and Papua New Guinea, and may also include Indonesian portions of New Guinea (*i.e.*, provinces of Papua and West Papua/Irian Jaya).

#### *Habitat/Ecology*

*Sousa sabulensis* occurs in shallow (2–5 m preferred) coastal marine and estuarine habitats, but also occasionally in dredged channels, and around reefs and offshore islands (Corkeron *et al.* 1997; Parra 2005; Parra *et al.* 2004, 2006). Little is known of their ecology, as only a few ecological studies have been conducted. Until the last few years, virtually all focused work on the species had been conducted in northeastern Australia (Queensland, *e.g.*, Parra 2005, 2006; Parra *et al.* 2006, 2011; Cagnazzi *et al.* 2011), and virtually nothing was known about the species in the western part of the country (Allen *et al.* 2012, Bejder *et al.* 2012). However, where individual social organization has been studied, like most other humpback dolphins, they appear to have a fission/fusion society with mostly short-term bonds beyond the mother/calf pair, and movements tend to be localized, although they may move into and out of bays on a regular basis (Parra *et al.* 2006, 2011; Cagnazzi *et al.* 2011). Some animals are permanent residents, with others more transitory, and group sizes in Cleveland Bay, Queensland, average about 3.5 individuals (Parra 2005).

#### *Life History*

There have been no detailed studies of life history in this species, but the small amount of information available suggests that it is similar to *S. chinensis* in most features (Heinsohn 1979). Very few external morphometric data are available for Australian humpback dolphins. Reported lengths were 100–270 cm ( $n = 58$ ), and 41 specimens  $\geq 200$  cm averaged  $232.8 \pm \text{SD } 19.17$  cm. Males  $\geq 200$  cm averaged  $237.7 \pm \text{SD } 18.21$  cm (range = 208–262 cm,  $n = 13$ ), and females averaged  $230.9 \pm 16.95$  cm (range = 200–260 cm,  $n = 18$ ). This suggests there might be slight sexual dimorphism in length. A live specimen (“Amity”) held captive at Sea World in Queensland

<sup>3</sup>Personal communication from I. Beasley, 24 Meethenar Street, Carlton, Tasmania 7173, Australia, 2013 to TAJ.

<sup>4</sup>Personal communication from F. Bonaccorso, Kilauea Field Station, PO Box 44, Hawaii National Park, HI 96718, U.S.A. 2012 to TAJ.

is suspected to be at least 48 yr of age (based on the fact that she was considered a young adult when captured and has been in captivity since at least 1974).<sup>5</sup> Australian humpback dolphins and Australian snubfin dolphins are largely sympatric throughout tropical Australia, and the two species interact frequently, with interbreeding and hybridization happening at least occasionally (Parra 2005, Kopps *et al.* 2013).

### *Etymology*

The species name, *sabulensis*, is based on the apparent range, over the Sahul Shelf extending between Australia and the island of New Guinea. The suggested common name is the Australian humpback dolphin, which refers to the main area of its known range, and the source of virtually all information available on this species to date.

### *Conservation Status*

There is no range-wide abundance estimate for this species, and although the conservation status in virtually all areas of the range is unknown, abundance has been estimated for a few populations. Most work has been done in northeastern Australia (Queensland; see Parra 2005). In Cleveland Bay, there are fewer than 100 individuals (Parra *et al.* 2006), and about 150 reportedly occur in two somewhat-discrete communities in the Great Sandy Strait Marine Park area (Cagnazzi *et al.* 2011). These estimates add up to the total of just a few hundred individuals, and it is unlikely that this species numbers more than a few thousand overall, perhaps much less. In northwestern Australia, there are no available abundance estimates, although ecological studies have started there in recent years (Allen *et al.* 2012, Bejder *et al.* 2012). The area of the Northwest Cape, Western Australia, has been reported to be a “hotspot” of humpback dolphin occurrence (Brown *et al.* 2012). Although there is no confirmation, Corkeron *et al.* (1997) speculated that humpback dolphins may generally be in decline in Australian waters. Known and potential threats include habitat loss and degradation, effects of overfishing, direct takes (both illegal killing and live capture), incidental catch (including in anti-shark nets in New South Wales), pollution, epizootics, vessel traffic, and wildlife tourism (Bannister *et al.* 1996, Parra *et al.* 2004, Parra 2005). In particular the northwestern portion of Australia is undergoing rapid development, with port facilities construction for oil, gas, and mining operations. *Sousa* populations in this area have been very poorly studied, but are thought to be small and vulnerable, and they are clearly in need of increased status assessment and better management efforts (Allen *et al.* 2012, Bejder *et al.* 2012, Brown *et al.* 2012). There are several large marine protected areas in the tropical waters of Australia, but in general these may not provide adequate protection for the critical habitat areas of this species (Parra 2005). The Australian action plan for cetaceans lists several needed conservation and management actions (Bannister *et al.* 1996) that have not been fully realized, and these are all the more important since it is now considered that the Australian animals are a separate species from those in Asia. Although prospects for populations along the Queensland coast are considered good, it is recognized that management efforts must be “intensive and adaptive” (Parra 2005).

<sup>5</sup>Personal communication from W. Blanshard, Sea World of Australia, Sea World Drive, Main Beach, Gold Coast, Queensland 4210, Australia, 2014 to TAJ.

## CONCLUSIONS

After reviewing the available evidence from osteology and genetics (including phylogenetic analyses), coupled with coloration and external morphology traits and features, a much clearer picture is now available of the taxonomy of humpback dolphins (see Table 2). Information from multiple lines of evidence, coming from several independent studies, all confirm what many have believed for some time. This is that the genus *Sousa* is composed of several different species, each with unique morphology and coloration patterns, and these species have been long separated, and are on different evolutionary tracks.

It might be considered surprising that there are not stronger morphological differences among the four species, considering their apparent long history of divergence. In fact, interspecific differences among the four species are mostly minor variations on a theme, with the exceptions of variation in skull shape, tooth counts, and development of the dorsal hump. This presumably results from the similar habitats (*i.e.*, warm, coastal, shallow waters) the species occur in throughout the range of the genus.

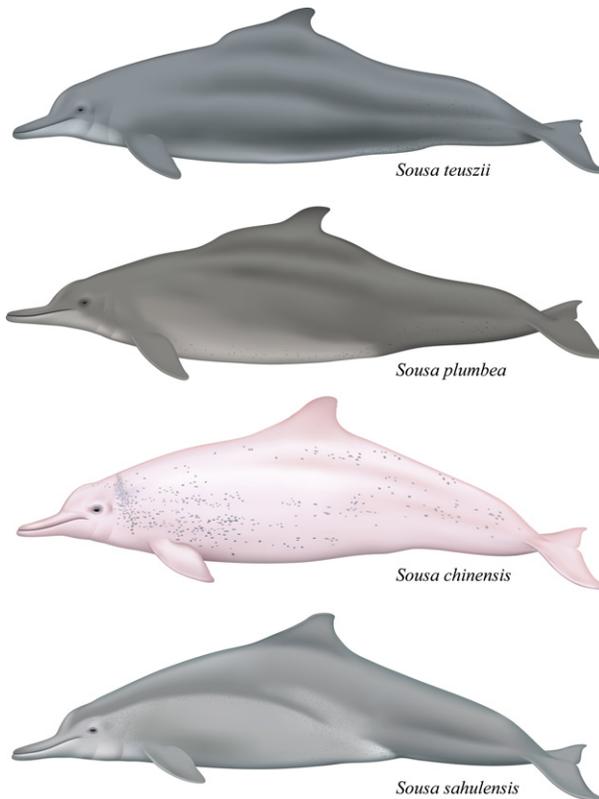


Figure 14. Composite sketches of the external morphology and coloration showing the typical appearance of the four species of humpback dolphins. Illustrations are of young adult males, all drawn to the same scale. Illustration by U. Gorter.

The most recent range-wide sampling and analysis of multiple lines of evidence provides clearcut evidence for species-level differences within the genus *Sousa*. Taking all the available information into account, we propose that the genus *Sousa* should now be divided into four species, as first proposed by Mendez *et al.* (2013) and recently recognized by the Society for Marine Mammalogy's Ad Hoc Committee on Taxonomy (Committee on Taxonomy 2014). These are: *Sousa teuszii*, the Atlantic humpback dolphin off West Africa; *Sousa plumbea*, the Indian Ocean humpback dolphin; *Sousa chinensis*, the Indo-Pacific humpback dolphin; and *Sousa sabulensis*, the newly described Australian humpback dolphin. Known differences among the four species are summarized in Table 2, and their external appearance is compared in Figure 14. Until there are additional lines of evidence for other taxonomic revisions at the species and subspecies levels, this review provides the information that best clarifies the taxonomy, nomenclature, biology and respective distribution of humpback dolphins throughout their range.

The recognition of this new view of the taxonomy of humpback dolphins, with at least four species and probably several subspecies within these, necessitates a reexamination of their conservation status and management actions. Clearly, the IUCN Red List designations for the four species will need to be assessed or revised, and the national status listings of many countries (*e.g.*, Australia, China, South Africa) will also need to be reexamined in light of this new knowledge. We also suggest that well-known populations of *Sousa* (subpopulations in IUCN parlance) that currently do not have a Red List assessment (*e.g.*, the Hong Kong/Pearl River Estuary population of *S. chinensis*) be evaluated under the IUCN criteria. Humpback dolphins have long been recognized as vulnerable to coastal development, fisheries, and vessel-traffic related threats, and if the full potential of genetic diversity of the genus is to be properly preserved, many changes will need to be made in how we manage and conserve these animals. While some populations have shown themselves to be remarkably resilient to habitat-related changes (*e.g.*, the Hong Kong/Pearl River Estuary population), there is evidence that these animals are reaching or have reached the limits of population viability, a notable concern for scientists studying them, and a red flag for management authorities charged with protecting them.

It has taken the accumulation of information from many years of collection of morphological data, and of the most complete range-wide sampling for molecular genetic material to date, so that a fairly complete picture of the patterns of variation and *Sousa* taxonomic relationships can finally be discerned. Admittedly, there are still many gaps in our knowledge and certain pieces of information are still missing, but we feel it is important to provide this proposed revision of the genus *Sousa* at this time, especially when one considers the significant threats facing humpback dolphins throughout most of their range and the current lack of adequate management of evolutionary units of biological diversity. Future work may yield additional insights into the genus *Sousa*, especially the existence of populations or subspecies in areas where there is currently a low representative sample of specimens. Critical locations from which samples are most urgently needed to clarify taxonomic questions are the southern coast of India, Sri Lanka, the northern Bay of Bengal, and the Indo-Malay region (especially the eastern islands of Indonesia).

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## SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12152/suppinfo>.

*Appendix S1*. Museum and collection acronyms.

*Appendix S2*. Specimens examined and referred.

## Corrigenda

p. 1516, last paragraph – “There are apparently regional pockets of relatively high density, such as Senegal/Gambia, Guinea Bissau/Guinea/Sierra Leone, Gabon/Congo, and Cameroon/Angola” should read “There are apparently regional pockets of relatively high density, such as Senegal/Gambia, Guinea Bissau/Guinea, and Gabon/Congo”.

p. 1517, second paragraph and p. 1526, second paragraph – “holtype” should read “holotype”.

p. 1519, *Distribution* – Existing *Sousa* records from Myanmar (Burma) are not confirmed to be *S. plumbea*, so that country should not be listed under confirmed records. Also, Bangladesh should not be listed.

p. 1524, *Distribution* – Myanmar (Burma) should not be listed under confirmed records.

p. 1527, last paragraph – “lenghts” should read “lengths”.

p. 1528, last paragraph – “Exmouth Bay” should read “Exmouth Gulf”.

Figure 4 – For *Sousa chinensis*, the frequency count of 53 vertebrae should be 1, not 2.

Supplementary Material, Appendix 2 – “*Sousa salulensis*” should read “*Sousa sahulensis*”.