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Diagnosability and description of a new subspecies of Indo-Pacific humpback dolphin, *Sousa chinensis* (Osbeck, 1765), from the Taiwan Strait

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Abstract

Background: Subspecies recognition can affect how people (scientists and non-scientists alike) view organisms and thus has important implications for research on, as well as the conservation of, these entities. Recently, a small group of Indo-Pacific humpback dolphins was discovered inhabiting the waters off central western Taiwan. This geographically isolated population possesses pigmentation patterns that are subtly, but noticeably, different from their nearest conspecifics in the neighbouring waters of the Jiulong River Estuary and Pearl River Estuary of mainland China. Due to this population's low and declining numbers and the numerous threats it faces, it was assessed as critically endangered by the Red List of Threatened Species of the International Union for Conservation of Nature. The purpose of this study is to examine the degree of differentiation of the Taiwanese population to determine if subspecies recognition is warranted.

Results: Analysis of the degree of differentiation in pigmentation patterns revealed nearly non-overlapping distributions between dolphins from Taiwanese waters and those from the Jiulong River + Pearl River estuaries of mainland China (the nearest known populations). The Taiwanese dolphins were clearly diagnosable from those of the Jiulong River + Pearl River estuaries under the most commonly accepted '75% rule' for subspecies delimitation (with 94% of one group being separable from 99+% of the other). Evidence of geographical isolation and behavioural differences also provided additional support for the distinctiveness of the Taiwanese dolphins.

Conclusions: Together, the evidence strongly demonstrated that the Taiwanese humpback dolphin population is differentiated at the subspecies level and on an evolutionary trajectory that is independent from that of dolphins from adjacent waters of mainland China (i.e. Jiulong River + Pearl River estuaries). As a result, the taxonomy of *Sousa chinensis* was revised to include two subspecies: the Taiwanese humpback dolphin, *Sousa chinensis taiwanensis* subsp. nov., and the Chinese humpback dolphin, *Sousa chinensis chinensis* (the nominotypical subspecies). These subspecies are described, and the holotype and paratype specimens for *S. c. taiwanensis* are established.

Keywords: Indo-Pacific; Taiwanese; Humpback dolphin; New subspecies; *Sousa chinensis taiwanensis*; Diagnosability; '75% rule'

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Background

The value and importance of subspecies (versus other intraspecific designations, such as populations, evolutionarily significant units and distinct population segments) as a unit of organization in biology have been the subject of great debate (e.g. see Mayr 1982; Ryder 1986; Zink 2004; Phillimore and Owens 2006; Patten 2010; Remsen 2010). Some have argued that most of the criticism plaguing subspecies has been due to inconsistent and subjective delimitation of subspecies, most of which were established decades ago when analytical abilities were very limited and have not been re-examined since (see Patten and Unitt 2002; Remsen 2010). Although the subspecies debate is beyond the scope of this paper, we agree that when delimiting subspecies (or any other taxonomic unit), objective quantitative testing of clear hypotheses based on a specified conceptual framework is scientifically sensible and will result in less controversy. Furthermore, this will allow practicing taxonomists to determine if explicit criteria are satisfied without the need for personal philosophical views to be involved or to be forced into more esoteric debate about subspecies as a taxonomic entity.

The subspecies category is the only non-species taxonomic rank that is accompanied by formal taxonomic treatment, scientific (trinomial) naming and establishment of type specimens, and recognized and governed by the International Code of Zoological Nomenclature (ICZN 1999). In this regard, it is treated similarly to species. For conservation biologists and resource managers, subspecies designations can also be useful for drawing attention to or prioritizing resource allocation for protection of threatened unique biological entities (Haig et al. 2006). Several national and international lists of threatened wildlife recognize subspecies, and inclusion on such lists can have important legal and financial ramifications (Haig et al. 2006). Recognition of endemic taxa can often result in local citizens developing an increased sense of ownership of, pride towards, and also conservation responsibility for such wildlife. For example, in Taiwan, endemic subspecies such as the Formosan landlocked salmon *Oncorhynchus masou formosanus* (often referred to as the 'National Treasure Fish') and the Formosan black bear *Ursus thibetanus formosanus* are much celebrated and attract considerable attention from local citizens, news media, conservation groups, scientists and government agencies. Furthermore, subspecies are entrenched in some important wildlife conservation policy and thus have legal status (e.g. US Endangered Species Act, Wildlife Conservation Act of Taiwan, Canada's Species at Risk Act). Therefore, ignoring subspecies designations because of personal philosophy can be damaging to the conservation of some taxa because they may not receive the same recognition and attention as similarly distinct taxa that possess trinomial names.

Because cetaceans are charismatic, high-profile animals, it may be somewhat surprising that they are 'under-classified' with respect to the number of subspecies (i.e. many more subspecies likely exist than are recognized presently) (Reeves et al. 2004; BL Taylor, personal communications). The main reason for this apparent taxonomic deficit is that traditionally, evidence for recognizing cetacean subspecies has been primarily a combination of morphological differences and geographic separation. However, obtaining a sufficient series of specimens for many taxa is difficult or nearly impossible given their large size and often rarity. This shortcoming of the present taxonomy of cetaceans can have negative consequences for understanding evolutionary histories within this group and for their conservation because attention and resources may not be allocated optimally.

Definition of subspecies

Subspecies are generally considered to be a population or populations within a species that are found in different breeding locations (allopatry) and have been equated to 'geographic varieties'. A commonality among most, if not all, subspecies definitions is that subspecies represent groups that are diagnosably distinct rather than just exhibiting mean differences (e.g. see Mayr and Ashlock 1991; Patten and Unitt 2002). The most common operational definition of subspecies is based on an arbitrary '75% rule'. The origin of this rule is uncertain but was discussed and adopted by Amadon (1949) to mean that a population should only be recognized as a subspecies if the following conditions are met. For a given defining character or set of characters, 75% of one population is distinguishable from more or less all (99+%) members of another population (and vice versa). Another interpretation of the '75% rule', with 75% of one population's distribution lying outside 75% of the distribution of another population, was rejected by Amadon (1949) as being too easily satisfied.

During a workshop on the shortcomings of cetacean taxonomy in relation to the needs of conservation, the participants observed that subspecies can include two types of entities: those that may not differ enough to be considered species and those that should be species but insufficient data exist to justify species level distinction (Reeves et al. 2004). The following general descriptive guidelines for designating cetacean subspecies were also adopted, '[i]n addition to the use of morphology to define subspecies, the subspecies concept should be understood to embrace groups of organisms that appear to have been on independent evolutionary trajectories (with minor continuing gene flow), as demonstrated by morphological evidence or at least one line of appropriate genetic evidence. Geographical or behavioural differences can complement morphological and genetic evidence for establishing subspecies. As such, subspecies could be geographical forms or incipient species'.

Humpback dolphins, genus *Sousa*

There is uncertainty about the number of species within the genus *Sousa* (see review by Jefferson and Rosenbaum 2014). Until recently, the most widely accepted view was of two species: Indo-Pacific humpback dolphin, *Sousa chinensis*, and Atlantic humpback dolphin, *Sousa teuszii* (see Jefferson and Van Waerebeek 2004). However, mounting molecular and morphological evidence suggested that taxonomic revision was needed (see Frère et al. 2008, 2011; Mendez et al. 2013) and led to a new proposed arrangement that included four species within the genus (Jefferson and Rosenbaum 2014). *Sousa teuszii* remained unchanged while what previously comprised *Sousa chinensis* was divided into the Indo-Pacific humpback dolphin (*S. chinensis*), the Indian Ocean humpback dolphin (*S. plumbea*), and a newly described species, the Australian humpback dolphin (*S. sahulensis*). Due to concerns about poor sampling from important areas in these studies, this new four-species arrangement was accepted only conditionally by the Taxonomy Committee of the Society for Marine Mammalogy (2014). Although several subspecies were also suggested, none were formally described.

Humpback dolphins in Chinese waters

Regardless of the two- or four-species arrangements for *Sousa*, humpback dolphins found in Chinese waters remain firmly ensconced within *S. chinensis*. The type locality of *S. chinensis* is the Canton (=Pearl) River Estuary, where Osbeck (1765) observed this 'snow-white' dolphin swimming and named it *Delphinus chinensis*. However, no scientific specimen was available until 1867, when Robert Swinhoe collected a specimen from the waters of Quemoy (=Chinmen Island) in the Jiulong River Estuary that was later described in detail by Flower (1870) and named *Delphinus sinensis*. The nomenclature was later revised to the present name *S. chinensis* by Allen (1938). In Chinese waters, several populations of Indo-Pacific humpback dolphins have been suggested (Jefferson 2000; Jefferson and Hung 2004), but no studies have unambiguously confirmed the structure and boundaries of these provisional populations with the exception of the Taiwanese humpback dolphins (see below) and no subspecies have been described.

In 2002, a population of humpback dolphins, inhabiting the coastal nearshore waters off central western Taiwan (=eastern Taiwan Strait), was discovered (see Wang et al. 2004a) (Figure 1). The Taiwanese humpback dolphins are clearly closely related to others found in Chinese waters and exhibit the same typical general characteristics (i.e. lacking an obvious hump at the base of the dorsal fin and with older adults being pinkish white in colouration - see Jefferson and Karczmarski 2001; Jefferson and Van Waerebeek 2004; Jefferson and Rosenbaum 2014). A quantitative study of pigmentation differences revealed that the geographically isolated Taiwanese dolphins are phenotypically distinct from its nearest known neighbours, found in the Jiulong River and Pearl River estuaries (Wang et al. 2008a). The Taiwanese population appears to be a year-round resident (Wang and Yang 2011) with a highly restricted distribution (Wang et al. 2007) and comprises fewer than 100 individuals (Wang et al. 2007, 2012). Unfortunately, this small isolated population is facing numerous existing (and looming) threats to its continued existence (see

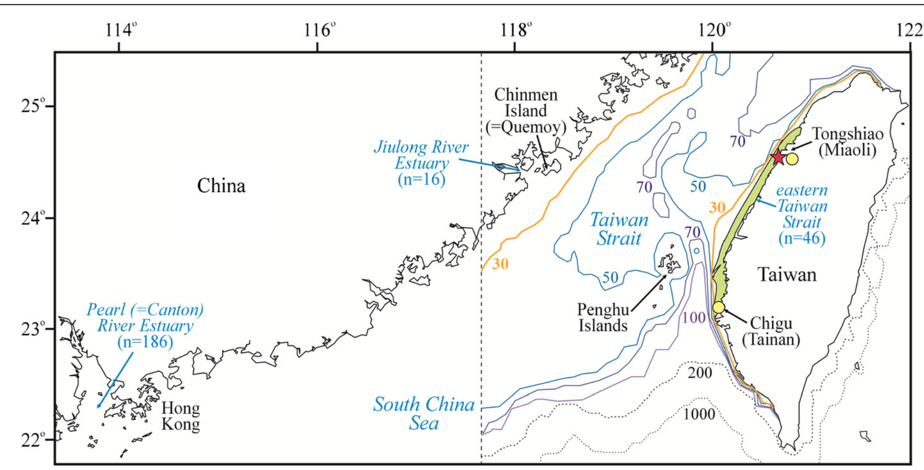

Figure 1 Map of the study area. Sampling locations of Indo-Pacific humpback dolphins analysed in this study. The green shaded area represents the known distribution of these dolphins, and the red star and yellow circles show the locations from where the holotype and paratype specimens of the Taiwanese humpback dolphin *Sousa chinensis taiwanensis* were collected, respectively. Some bathymetric contours in the Taiwan Strait are also shown.

Wang et al. 2004b; Ross et al. 2010; Dungan et al. 2011; Slooten et al. 2013), and an assessment of this population against the criteria of the IUCN Red List of Threatened Species resulted in a 'critically endangered' status (Reeves et al. 2008). The population's current very low potential biological removal level (Slooten et al. 2013) and precarious viability under various likely scenarios (Araújo et al. 2014; Huang et al. 2014) further confirm the direness of its Red List status.

In the original pigmentation study by Wang et al. (2008a), the degree of differentiation was not examined to determine if subspecies level recognition was warranted. The main purpose of this study was to rectify the oversight of the previous study by conducting a quantitative and objective analysis to determine if the Taiwanese population deserves subspecies recognition. We re-examine the pigmentation data of Wang et al. (2008a) (with additional new data) to test the null hypothesis that the Taiwanese humpback dolphins are not diagnosably distinct from those of the Jiulong River and Pearl River estuaries. We also compare osteological data from three Taiwanese specimens with published data on mainland Chinese humpback dolphin specimens and review available information on the species to better understand the degree of isolation that exists between these groups of dolphins.

Methods

Pigmentation

The raw scores of the spotting intensities on dolphin bodies and dorsal fins in Wang et al. (2008a) were re-examined. This dataset did not include completely grey individuals with little to no spotting (i.e. young calves and juveniles), which appeared to show no differences among the dolphins of the Pearl River Estuary, Jiulong River Estuary and eastern Taiwan Strait. Scores were obtained from nine independent observers who determined spotting intensity on a scale from 1 (least spotted) to 4 (most intensely spotted) for the bodies and dorsal fins of individual dolphins by examining photographs (for more details, see Wang et al. 2008a). To reduce the likelihood of various observer errors (e.g. mistakes due to data entry, fatigue, etc.), we excluded the high and low scores before calculating the means for each specimen. (However, including the high and low scores as in Wang et al. 2008a had no noticeable effect on the main results). Re-examination of the photographs used in Wang et al. (2008a) resulted in two eastern Taiwan Strait specimens being omitted from the present analyses. One specimen was excluded due to poor photographic quality, and the other specimen was eliminated because it represented the other side of an individual already in the dataset [note: since the study by Wang et al. (2008a), photographs of both sides of every individual in the Taiwanese population have been obtained by the authors so it was possible to confirm the double inclusion of this individual; none of the other specimens analysed presented this problem]. The total number of different individual dolphins examined in the present study was 248 with 186 from the Pearl River Estuary, 16 from the Jiulong River Estuary and 46 from the eastern Taiwan Strait (Figure 1). Of these, 6 and 17 new individuals from the Jiulong River Estuary and eastern Taiwan Strait, respectively, were photographed after Wang et al. (2008a) and added to the present study.

The photographs used in this study were primarily from individual identification catalogues. All photographs examined were of the two highest quality categories as described in Wang et al. (2012).

Data analyses

We repeated the statistical analyses of the previous study (Wang et al. 2008a) on the expanded dataset to determine if the main results remained unchanged. These analyses included multiple pairwise *t*-tests and one-way analysis of variance (ANOVAs) with *post hoc* comparisons (least significant difference, Scheffe's, Duncan's multiple range, Tukey's honestly significant difference and the Newman-Keuls methods). The level of significance for all tests was 0.05, but for the multiple pairwise *t*-tests, the critical threshold values were corrected using the sequential Bonferroni method (Rice 1989).

Because the main focus of this study was to examine the degree of differentiation between the Taiwanese humpback dolphins and those of their nearest known neighbours in mainland Chinese waters, the dolphins of the Jiulong River and Pearl River estuaries were pooled for the main analyses of this study. Given the small number of Jiulong River Estuary dolphins available in this study, keeping them in a separate group for comparison and diagnosability tests (see below) would not have been meaningful. Pooling was also supported by the findings of Wang et al. (2008a) and the analyses of the expanded dataset in this study (see 'Results'), which showed that Jiulong River Estuary dolphins were not significantly different or distinguishable from Pearl River Estuary dolphins in the pigmentation characters examined (Figure 2).

To better understand the degree of differentiation in the pigmentation of the Taiwanese and Jiulong River Estuary + Pearl River Estuary dolphins, we performed a discriminant analysis on the two variables (spotting intensities on the body and dorsal fin). Although the percentage of misclassifications can be used as a metric for how well specimens can be discriminated, merely reporting percent correct classifications from discriminant analyses was argued to be insufficient by Patten and Unitt (2002). Therefore, the discriminant scores of the specimens were analysed to determine if Taiwanese dolphins were diagnosably different

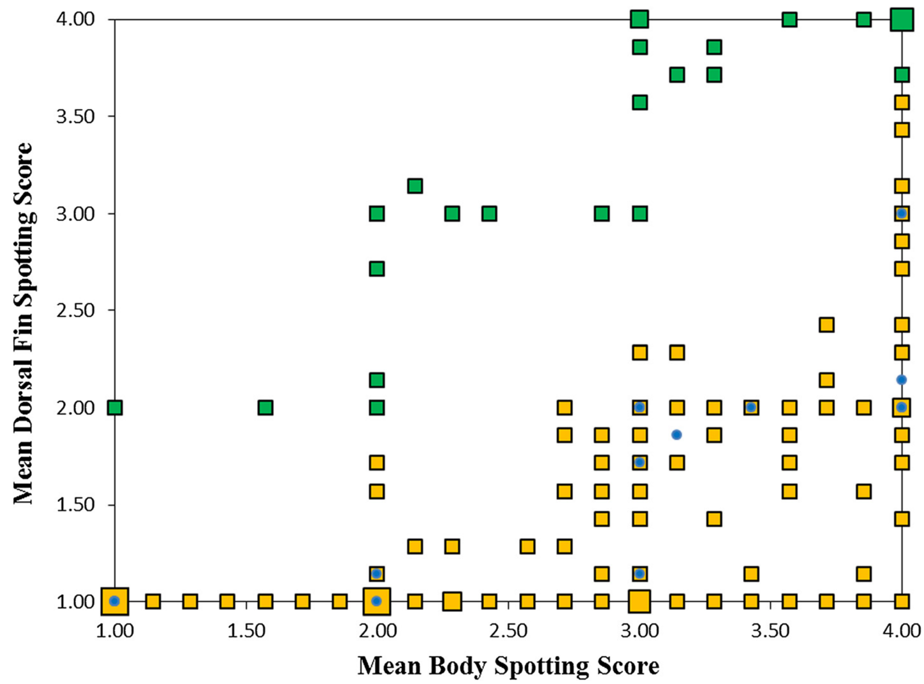

Figure 2 Scatterplot of spotting intensity on dorsal fins and bodies of Indo-Pacific humpback dolphins. Mean scores of the spotting intensities on the dorsal fins vs. bodies of Indo-Pacific humpback dolphins from the eastern Taiwan Strait (green squares), Pearl River Estuary (yellow squares) and the Jiulong River Estuary (blue circles). Small symbols = 1 to 5 individuals; medium symbols = 6 to 10 individuals; large symbols = >10 individuals.

from those of the Jiulong River Estuary + Pearl River Estuary (see diagnosability analysis below).

All statistical analyses were performed using STATISTICA version 12 (Statsoft, Inc. 2014, www.statsoft.com).

Diagnosability analysis for subspecies

With the possible exception of characters that are clearly and completely non-overlapping between two groups, diagnosability testing should be conducted to determine subspecies status in an objective and quantitative manner. To the best of our knowledge, Baker et al. (2002) was the first and only study that explicitly tested diagnosability under the operational definition of the '75% rule' for identifying a cetacean subspecies (in this case, Maui's dolphin, *Cephalorhynchus hectori maui*). To determine if the pigmentation exhibited by Taiwanese humpback dolphins was diagnosable from those of the Jiulong River Estuary + Pearl River Estuary, and hence supporting distinct subspecies, we also used the diagnosability index (*D*) of Patten and Unitt (2002) with the same interpretation of the operational definition ('75% rule') for subspecies as in Baker et al. (2002). Thus, for two groups to qualify as different subspecies, 75% of the distribution of one group must lie outside 99% or more of the other (and this must also be true when testing in the opposite direction - see Patten and Unitt 2002).

Osteology

For thoroughness, we also examined five new, complete (or nearly complete) skeletons of physically mature specimens from the eastern Taiwan Strait ($n = 3$) and Hong Kong's waters of the Pearl River Estuary ($n = 2$). Twenty-two of the cranial morphometric and meristic characters analysed in Jefferson and Rosenbaum (2014) were measured on the new specimens by JYW following Perrin (1975). Tooth counts were based on the largest number of alveoli counted in a single tooth row, and vertebral counts followed the sections described by Rommel (1990). Due to the small sample size, we only conducted simple comparisons with published data on specimens from mainland Chinese waters (Flower 1870; Huang et al. 1978; Wang and Sun 1982; Wang and Han 1996; Wang 1999; Zhou 2004; Jefferson and Van Waerebeek 2004; Jefferson and Rosenbaum 2014). Data on the proposed neotype for *S. chinensis* (Porter 2002) were excluded from this study due to serious concerns about the information presented as well as the specimen being immature (see Jefferson and Van Waerebeek 2004; Jefferson and Rosenbaum 2014).

Results

Pigmentation

Repeating the same analyses that were conducted by Wang et al. (2008a) but on the expanded dataset did not produce any real notable differences from previous results. However, the body spotting on the dolphins of the eastern Taiwan Strait and that on dolphins of the Pearl River Estuary were nearly significantly different (the *p* value was equal to the alpha, after sequential Bonferroni correction for multiple tests), whereas in the original study, differences in body spotting between dolphins from these two regions were not significant. The eastern Taiwan Strait dolphins had significantly greater dorsal fin spotting intensity and greater difference between the spotting on the dorsal fin and body than Jiulong River Estuary or Pearl River Estuary dolphins (all $p < 0.0001$), while neither of these characters were significantly different between dolphins of the Jiulong River Estuary and Pearl River Estuary (see Additional file 1 for detailed results of these analyses).

Not surprisingly, the discriminant analysis also showed very clear separation of the Taiwanese dolphins from the Jiulong River Estuary + Pearl River Estuary (pooled) dolphins (Wilk's lambda = 0.307, $F_{2,245} = 276.25$, $p < 0.0001$) with very little overlap (Figure 3) and thus provided more confirmation that the Taiwanese dolphins were differentiated. [Note: a discriminant analysis was also conducted on the original data, without the new specimens, which were reserved for cross-validation of the classification functions. The overall results were the same as above (Wilk's lambda = 0.376, $F_{2,222} = 183.90$, $p < 0.0001$), and the classification functions generated by the analysis correctly assigned 20 of the 21 (95.2%) new specimens to the region from which they originated].

Examination of the data (body spotting, dorsal fin spotting and discriminant scores) did not reveal any significant deviations from normality or heteroscedasticity. Furthermore, there were no specimens with unusually large or small values in the original or discriminant scores to overly influence the means and variances, so correlations between these two parameters are unlikely.

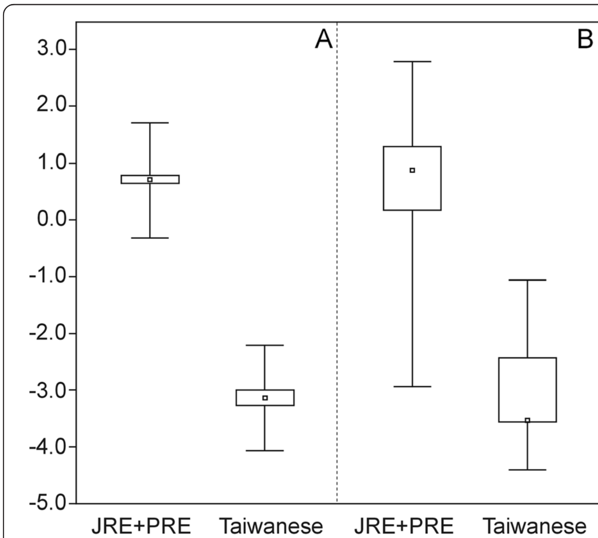

Figure 3 Box and whisker plots of canonical scores for Indo-Pacific humpback dolphins. The squares, boxes and whiskers represent means, standard errors and standard deviations, respectively, in **(A)** and medians, 25 and 75 quartiles and minima-maxima, respectively, in **(B)**. Indo-Pacific humpback dolphins from the Jiulong River Estuary + Pearl River Estuary (JRE + PRE) and Taiwanese waters.

The diagnosability indices provided clear evidence supporting subspecies recognition for the Taiwanese humpback dolphins following the '75% rule' ($D_{\text{eastern Taiwan Strait, Jiulong River Estuary + Pearl River Estuary}} = 0.91$ and $D_{\text{Jiulong River Estuary + Pearl River Estuary, eastern Taiwan Strait}} = 0.83$). In a mathematically similar manner as explained by Baker et al. (2002), we also estimated the percentage separation between the Taiwanese and Jiulong River Estuary + Pearl River Estuary dolphins using the formula of Patten and Unitt (2002). We found that the Taiwanese humpback dolphins were diagnosable from those of the Jiulong River Estuary + Pearl River Estuary at a very high level (94% from 99+%) (Figure 4).

Descriptive diagnosis

Differences in pigmentation between the Taiwanese and Jiulong River Estuary + Pearl River Estuary humpback dolphins can be best and most easily differentiated by dividing dolphins into two categories of spotting on their bodies. For dolphins with little to no spotting on the body, score = 1; all dolphins from the Jiulong River Estuary + Pearl River Estuary had less to no spotting on their dorsal fins (of 27 Jiulong River Estuary + Pearl River Estuary dolphins with a body spotting score of 1, 22 had bodies and dorsal fins that were both unspotted (Figure 5A), 5 had dorsal fins with noticeably less spotting, but none had a more spotted dorsal fin). There was only one eastern Taiwan Strait dolphin with a body score of 1 in the original dataset, and its dorsal fin was more spotted than its body. Supporting this pattern was another three eastern Taiwan Strait dolphins from the original dataset that have since lost enough spotting on their bodies to fit the category of little to no spotting (score = 1), and all have spotted dorsal fins (Figure 5B).

For dolphins with obvious spotting on the bodies, score = 2, 3 or 4; 96% and 98% of the specimens from the eastern Taiwan Strait and Jiulong River Estuary + Pearl River Estuary, respectively, would be correctly classified based on the spotting intensity on the dorsal fin being either 1) equal to or more than that on the body or 2) noticeably less than that on the body. The typical pattern for Jiulong River Estuary + Pearl River Estuary dolphins is that the dorsal fin is usually noticeably less spotted than the body (Figure 5C), whereas for eastern Taiwan Strait dolphins, the dorsal fin is equally or more intensely spotted than the body (Figure 5D). The observed frequencies of specimens divided into these categories of spotting intensity on the dorsal fin relative to

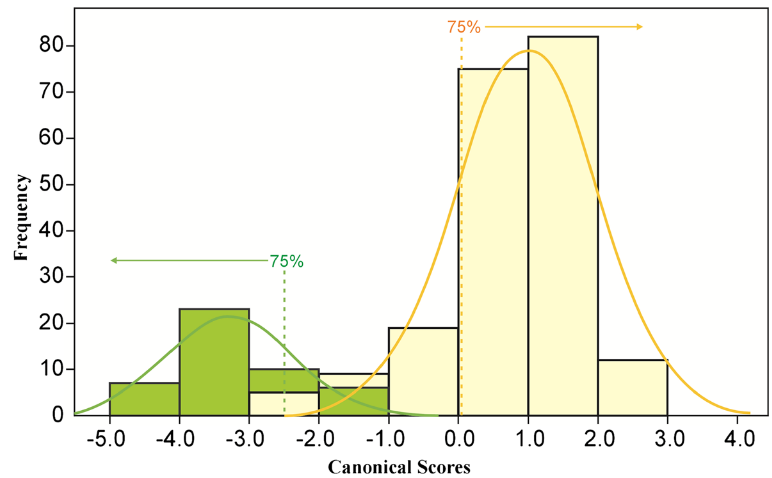

Figure 4 Frequency distributions of canonical scores of Indo-Pacific humpback dolphins. The distributions for Indo-Pacific humpback dolphins from Taiwanese waters and the Jiulong River Estuary + Pearl River Estuary are shown in green and yellow, respectively. The dotted lines indicate the locations where 75% of the distributions are found.

the body (Table 1) were significantly different ($p << 0.0001$, Fisher's exact test) between the eastern Taiwan Strait and Jiulong River Estuary + Pearl River Estuary. Furthermore, including the dolphins with little to no spotting on the bodies (score = 1) did not change these results ($p << 0.0001$, Fisher's exact test).

[Note: The lack of unspotted individuals in the eastern Taiwan Strait may be seen as reflecting a difference in age structure between the dolphins of Taiwanese waters and the Jiulong River Estuary + Pearl River Estuary (i.e. fewer Taiwanese dolphins are reaching an old enough age to become completely unspotted). However, we believe that becoming completely unspotted is not a characteristic shared by the Taiwanese population. All three stranded Taiwanese specimens had some spotting even though they were physically mature. Also, several of the least spotted adult Taiwanese dolphins (body scores = 2) have been monitored annually for more than 10 years, and minimal changes in their overall spotting intensity have been observed (JY Wang, unpublished observations). Regardless, even if there was a lack of the oldest individuals in the eastern Taiwan Strait population, the distinguishing pigmentation feature (i.e. the relationship between the spotting intensity on the dorsal fin and that on the body - best visualized in Figure 2), remains unaffected].

Osteology

Published data from a total of 38 specimens from mainland Chinese waters were included for comparison in

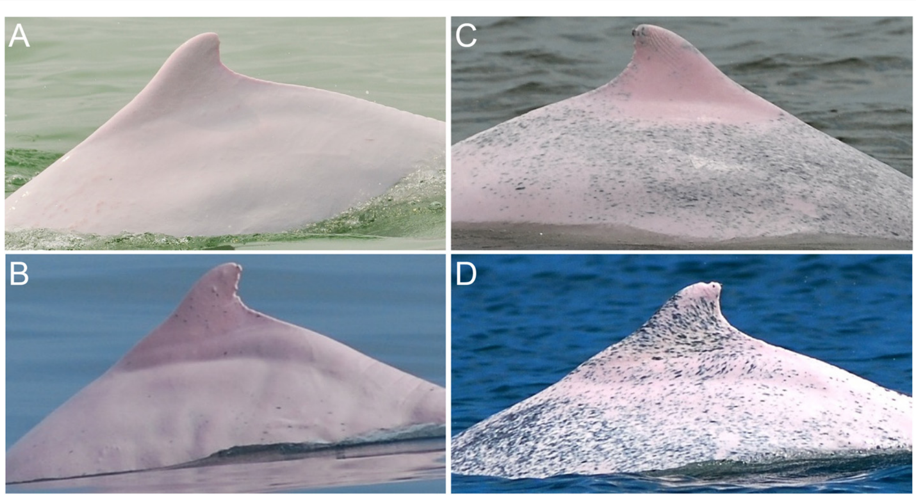

Figure 5 Typical Indo-Pacific humpback dolphins with unspotted and spotted bodies. Photographs of Indo-Pacific humpback dolphins from the Pearl River Estuary **(A, C)** and the eastern Taiwan Strait **(B, D)**. Photographs by J.Y. Wang/*FormosaCetus* Research and Conservation Group.

Table 1 Number of individual dolphins in categories based on relative spotting on dorsal fin versus body

	Dorsal fin spotting		Total
	≥ body	< body	
Eastern Taiwan Strait	43	2	45
Jiulong River Estuary + Pearl River Estuary	3	172	175

The dolphins in this table are individuals with obvious spotting on their bodies (score = 2, 3 or 4 in Wang et al. (2008a)). The dorsal fin spotting categories are as follows: spotting intensity on the dorsal fin is greater than or equal to that on the body, and spotting intensity on the dorsal fin is obviously less than that on the body. The observed frequencies were significantly different for the dolphins of the two regions ($p << 0.0001$, Fisher's exact test).

this study. Simple comparisons of data from the three Taiwanese specimens revealed no obvious differences in cranial characters (Additional file 2). For a few characters, absolute measurements of the Taiwanese specimens and Swinhoe's specimen described by Flower (1870) were slightly larger than the maximum published values. However, all proportions (relative to condylobasal length and the rostrum length to width ratio) were well within the minimum and maximum values reported. None of the post-cranial meristic values were beyond the reported data. Comparisons with the upper tooth counts versus length/breadth data in Figure three of Jefferson and Rosenbaum (2014) also showed no notable differences.

All three Taiwanese specimens had 52 vertebrae, whereas 17 specimens from mainland Chinese waters (including the two new Hong Kong and Swinhoe's specimens) had between 50 and 53 with a mode at 51 ($n = 9$). Only one specimen, from the Beibu Gulf, Beihai, Guangxi Province (Huang et al. 1978), had 53 vertebrae (note: Jefferson and Rosenbaum (2014) reported in error two specimens with 53 vertebrae - T.A. Jefferson, pers. comm.). This specimen was also reported to have 13 thoracic vertebrae, which is an unusual value for humpback dolphins from Chinese waters. Such outlying values suggest that this specimen should be re-examined. Although differences in the frequency distribution of vertebral counts may exist, more specimens (especially from the Taiwanese population) will be needed to test this hypothesis.

Other evidence

The preferred habitat of *Sousa* species is shallow (<30 m) coastal waters within a few kilometres of the shoreline, and at least in Chinese waters, humpback dolphins appear to have a close affinity to estuaries (see Ross et al. 1994; Zhou et al. 1995; Jefferson and Karczmarski 2001; Jefferson and Hung 2004; Jefferson and Rosenbaum 2014). With the exception of the narrow margins of inshore, estuarine waters along western Taiwan and mainland China, most of the Taiwan Strait (being deeper than 50 m and with considerable intrusions of oligotrophic oceanic waters from the Kuroshio and the South China Sea currents (see Jan et al. 2002)) does not possess the kind of habitat in which humpback dolphins are typically found. The shortest distance across the Taiwan Strait (which can be deeper than 70 m) between the Taiwanese population and nearest mainland Chinese humpback dolphins is about 180 km (Figure 1), whereas humpback dolphins tend to have minimal movement with linear distances of a few tens of kilometres (Hung 2000; Hung and Jefferson 2004). Although humpback dolphins in South African waters were reported to move across linear distances of up to 120 km (Durham 1994; Karczmarski 1996), these movements were always in shallow coastal waters along the shoreline and not over deep waters. Annual dedicated cetacean surveys in the eastern Taiwan Strait since 2002 have failed to record any humpback dolphins in waters deeper than about 30 m and beyond 3 km from the shoreline of western Taiwan (Wang et al. 2007; Ross et al. 2010; Dares et al. 2014). Even though there are many stranding, bycatch and sighting records of coastal small cetaceans (e.g. *Tursiops truncatus*, *T. aduncus*, *Neophocaena phocaenoides*, *Delphinus capensis*) from the Pescadores (=Penghu) archipelago, which is located between Taiwan and mainland China, there are no records of *Sousa* from these islands (Wang and Yang 2007). Furthermore, photographic identification of a large proportion of known Taiwanese individuals in the same waters year-round provided direct evidence that this population is almost certainly resident to the eastern Taiwan Strait (Wang and Yang 2011). Comparisons of the catalogues of humpback dolphins showed that no individual was common to both the eastern Taiwan Strait and the Jiulong River Estuary or the Pearl River Estuary (Wang et al. 2008a; Chou et al. 2013), which further supports the lack of exchange. The Taiwanese population has been well monitored annually by photo-identification methods since 2007. All non-calf individuals have been known since 2010, and there are no records of new individuals (with the exception of new calves), so there is no evidence of immigration from or emigration to adjacent populations. Finally, a comparative study on the social structure of humpback dolphins of the eastern Taiwan Strait and Pearl River Estuary showed that the Taiwanese dolphins also differed in social structure and organization (Dungan 2011; Dungan et al. 2012, 2015). When considered together, these many pieces of supplementary information provide strong supporting evidence for the lack of contemporary exchange of humpback dolphins across the Taiwan Strait.

Discussion

Colouration differences are important taxonomic characters for many species including cetaceans (e.g. Perrin 1972, 1975, 1990; Perrin et al. 1987; Heyning and Perrin 1994; Rosenbaum et al. 1995; Perrin 2009; Amano and Hayano 2007; Robineau et al. 2007). Complex colouration patterns (such as stripes and spotting) on individual cetaceans are not known to change with environmental conditions. None of the ephemeral or environmentally induced colour changes reviewed by Perrin (2009) for cetaceans apply to the pigmentation characters examined in this study, while there is some support for the genetic bases of colouration variation in cetaceans (e.g. Schaeff and Hamilton 1999; Ayoub et al. 2009; Polanowski et al. 2012). As such, the pigmentation differences in the humpback dolphins examined in this study are most likely to be phenotypic expressions of underlying genetic differences.

For *Sousa* species, Jefferson and Rosenbaum (2014) presented considerable descriptions of colouration differences between the species. However, they recognized that there was only one quantitative study of such differences (Wang et al. 2008a), which demonstrated subtle but clear differences between the Taiwanese and Jiulong River Estuary + Pearl River Estuary humpback dolphins. The present study fully corroborated the findings of this earlier pigmentation study (and with a larger dataset) but more importantly demonstrated that the Taiwanese population is diagnosably distinct from the dolphins of the Jiulong River Estuary + Pearl River Estuary and thus satisfied the '75% rule' for recognition as a subspecies. This was further supported by data on geographical separation, observations of the distribution of individuals and behavioural differences (i.e. in social structure - see Dungan 2011; Dungan et al. 2012, 2015). Moreover, the best available evidence shows that the Taiwanese humpback dolphin possesses the main features of subspecies (see Reeves et al. 2004; Patten 2010): they are restricted to the waters of western Taiwan, which means they are reproductively isolated (but note that reproductive isolation is not a prerequisite of subspecies, which by definition accepts or even expects some low level of continuing gene flow); the morphological differences that exist between the Taiwanese dolphins and their nearest neighbours are not clinal but are diagnosably distinct; the characters examined are not those that maybe environmentally induced (see Perrin 2009 for examples) but instead are likely a reflection of genetic and developmental differences; these features are consistent with the Taiwanese humpback dolphin being a lineage that is evolving independently from the dolphins of the Jiulong River Estuary + Pearl River Estuary. Although such lineages could also be considered distinct species under the unified species concept (de Queiroz 2007), we prefer to advocate subspecific designation until there is stronger evidence to elevate the status.

Zoogeography

Because of the coastal shallow water nature of the species, the biogeography of *S. chinensis* can be viewed more like that of a coast-dwelling terrestrial mammal than a typical pelagic marine species. It is most likely that humpback dolphins arrived at and were able to colonize the coastal waters of western Taiwan sometime during the last glacial maximum (about 17,000 to 18,000 years ago) when the sea level was much lower and the present-day Taiwan Strait was spanned by a land bridge (and its accompanying shallow waters) that connected the island of Taiwan to continental China and their associated coastal waters (e.g. see Voris 2000). It was likely that the shallow waters preferred by humpback dolphins appeared in the Taiwan Strait sometime just before the completion of the land bridge and allowed humpback dolphins to cross the 'deep' (relative to the preferred shallow water habitat of humpback dolphins) water barrier of the Taiwan Strait. Subsequent retreat of the ice resulted in increasing sea levels that first submerged the land bridge and then eliminated the shallow water conduit that permitted humpback dolphin movements across the Strait. The continuing deepening of the Taiwan Strait resulted in the effective isolation (geographically, behaviourally, reproductively and ultimately genetically) of the new colonizers of Taiwan. An interesting contrast with this biogeographical hypothesis, which resulted in the isolation of populations of *Sousa*, is that rising sea levels and the flooding of the Taiwan Strait during this period likely allowed secondary contact for newly formed finless porpoise (genus *Neophocaena*) species in this region after the land bridge barrier in the Taiwan Strait disappeared (Wang et al. 2008b).

Isolation of the Taiwanese humpback dolphins from those of mainland Chinese waters is likely to continue into the near future. With global climatic warming being observed and predicted into the future at least in the near and medium terms (hence further melting of polar ice and increasing sea levels), the Taiwan Strait will continue to deepen and further enhance this oceanographic barrier to movement of *Sousa* across the Taiwan Strait. Thus, it is reasonable to predict that the continued isolation of the Taiwanese humpback dolphins will further promote differentiation and, if sufficiently long, may even result in speciation.

Conclusions

Inconsistent descriptions, subjective conclusions, poor execution of delimitation criteria and lack of diagnosability testing have long plagued subspecies classifications. This has increased the amount of criticism levied against subspecies as being a useful level of biological organization. Although cetaceans may be under-classified with regard to the number of subspecies, this can actually be viewed as fortunate because much can be learned from the debates and experiences of researchers focused on other taxonomic groups that face the opposite problem (i.e. overclassification of subspecies). We believe that in order to build strong and objectively determined subspecies, future studies regarding cetacean subspecies should include diagnosability tests under clearly specified levels (or methods that are conceptually similar) as was used in Baker et al. (2002) and in the present study so that a common standard exists for determining subspecies across various taxonomic groups.

In the present study, clear diagnosability in pigmentation patterns between the humpback dolphins of Taiwanese and neighbouring waters was demonstrated in an objective and quantitative manner by using the method of Patten and Unitt (2002) for delimiting subspecies under the '75% rule'. Furthermore, additional supplementary lines of evidence also provided support for subspecies recognition. As such, we designate the geographically isolated and morphologically differentiated Taiwanese population of Indo-Pacific humpback dolphins as a new subspecies, *Sousa chinensis taiwanensis*. Consequently, all other humpback dolphins within *Sousa chinensis* are grouped into the nominotypical subspecies *Sousa chinensis chinensis*, until other subspecies can be demonstrated and described.

Subspecies descriptions

Order Cetartiodactyla Montgelard, Catzefils and Douzery 1997
Cetacea Brisson, 1762
Odontoceti Flower, 1867
Family Delphinidae Gray, 1821
Genus *Sousa* Gray, 1866

Sousa chinensis chinensis (Osbeck, 1765)

Holotype

The species was described by Osbeck (1765) from observing living animals, and because the practice of designating a holotype specimen was not in force at this point in history, no holotype exists; but the dolphins he observed would constitute syntypes (ICZN 1999). A near-complete skeleton of a physically mature specimen was acquired by Robert Swinhoe in 1867, thoroughly described and illustrated by Flower (1870), and would have been the prime candidate for designation as the neotype, if a need existed. Unfortunately, this specimen was destroyed during WWII (Pilleri 1979). Thus, no type specimen exists for the nominate subspecies. Although Porter (2002) proposed a neotype for *S. chinensis*, this endeavour failed to satisfy essential provisions in the International Code of Zoological Nomenclature (ICZN 1999) that govern neotype designation (Article 75, specifically 75.2, 75.3.1, 75.3.2 and 73.3.5). Given the detailed work presented by Flower (1870), there was (and still is) no controversy about the identity or type locality of this species and there was no 'exceptional need' (Article 75.3) for a neotype, as evidenced by the near absence of the reference to Porter's specimen in recent studies on *Sousa* taxonomy, including those co-authored by Porter (see Jefferson and Van Waerebeek 2004; Frère et al. 2008, 2011; Chen et al. 2008; Wang et al. 2008a; Chen et al. 2010; Lin et al. 2010, 2012; Mendez et al. 2013; Jefferson and Rosenbaum 2014). Not only was the proposed neotype not featured in these studies but also some authors specifically and directly recommended against comparisons to this specimen because of the unreliable information presented (see Jefferson and Van Waerebeek 2004; Jefferson and Rosenbaum 2014). Finally, with no examination of *Sousa* specimens from outside the type locality and by providing no new taxonomic information, the designation of the neotype by Porter (2002) can only be viewed as a curatorial exercise and hence is invalid (ICZN 1999) [a more detailed discussion about the invalidity of the proposed neotype and issues with the information presented in Porter (2002) is available in Additional file 3]. Any future need of reference specimens should consider the two complete adult topotype specimens from the Pearl River Estuary (SC03-08/09 and SC03-19/09) that were examined in this study as well as by Jefferson and Rosenbaum (2014). Presently, these topotypes and the detailed description of Swinhoe's specimen by Flower (1870) should be adequate to overcome the lack of a type specimen for this species.

Type locality

The species was first described from observing dolphins swimming in the Canton (=Pearl) River Estuary. Swinhoe's specimen that was described by Flower (1870) was collected from the waters of Quemoy (presently known as Chinmen Island) in the Jiulong River Estuary, which is roughly 500 km northeast of the Pearl River Estuary.

Etymology

The '*chinensis*' name refers to the general location from where the species was originally described. To maintain consistency with the scientific name of the subspecies, we suggest the following common names: Chinese humpback dolphin or the Chinese white dolphin (a direct translation of the most common local moniker, 'Zhonghua bai hai tun'). We recognize that before the present revision, Chinese white dolphin referred to the species. To avoid confusion, we recommend that Indo-Pacific humpback dolphin be retained as the common name for the species (following Jefferson and Rosenbaum 2014) while Chinese humpback dolphin or Chinese white dolphin is used in reference to the nominotypical subspecies *S. c. chinensis*. This nomenclatural arrangement should facilitate increased local acceptance and usage of the Indo-Pacific humpback dolphin name for the species because it does not negate the local common name for the local animals and would also allow easier (and logical) accommodations for any future subspecies that may be found within *S. c. chinensis* without the need to change the species' common name.

Diagnosis

This subspecies has complex pigmentation with dramatic developmental changes (see Jefferson et al. 2012; Jefferson and Rosenbaum 2014). It is medium to dark grey at birth and then transitions with age through various degrees of light and dark spotting while the base layer colour also changes from being primarily grey to white. In old individuals, spotting may completely disappear leaving only the white base colour, which may appear bright pink on living animals due to blood flushing to the surface of the skin. Young calves and juveniles (those possessing mostly grey pigmentation with little to no spotting) appear to be indistinguishable from the Taiwanese subspecies based on the characters examined in this study. For older individuals, the spotting intensity on the dorsal fin of this subspecies begins to diminish well before the spotting intensity on the area of the body adjacent to the dorsal fin. Thus, the colouration of the dorsal fin is less spotted (often strikingly so) and does not appear as a smooth continuation of the body pigmentation (Figure 5C). It is rare for dolphins with spotted bodies to have equal spotting intensity on the dorsal fin (only 3 of the 175 specimens examined), and none was observed to have a more intensely spotted dorsal fin. Very old dolphins from at least the Pearl River Estuary and Jiulong River Estuary can become completely spotless (both bodies and dorsal fin), and these appear to be mostly females, suggesting some sexual dimorphism in spotting loss (Figure 5A). It is important to note that dolphins in other parts of this subspecies range tend to exhibit much less white coloration, being primarily dark (see Jefferson and Rosenbaum 2014). It is likely that the present nominate subspecies comprises multiple undescribed subspecies (or possibly even species), but more research on pigmentation differences is needed to test this hypothesis.

Distribution

The nominate subspecies is found from the Yangtze River Estuary in central China south through Southeast Asia (east to at least Borneo) and extending west throughout the northern rim of the Indian Ocean to at least Orissa, India (Jefferson and Rosenbaum 2014). There appears to be at least eight major concentrations of this subspecies in the coastal waters of China (Jefferson 2000; Jefferson and Hung 2004), but others will almost certainly be found throughout the species' distribution. Further subspecies divisions are probable.

Sousa chinensis taiwanensis subsp. nov

Holotype

NMNS-14812 (=JYW-09-01). This was a physically mature (all vertebral epiphyses fused solidly to the centra) female about 250 cm in length and known to the authors since 2002 as 'TW-03' in the photographic catalogue of individuals of Taiwanese humpback dolphins (which was established in 2002 and maintained by the *FormosaCetus* Research and Conservation Group until 2013 when it was continued by the CetAsia Research Group). This was one of the least spotted and mostly pink individuals in the catalogue. Condylobasal length: 529.0 mm. The rostrum is curved slightly to the right. The lower jaw bones are unfused at the symphysis (but glued together) and also curve slightly to the right. Dental formula (alveolar counts): 34 or 35 (upper left), 33 or 34 (upper right), 31 or 32 (lower left), and 31 or 32 (lower right). Vertebral formula: Ce7 + T12 + L10 + Ca23 = 52 (the terminal caudal element counted as one vertebra). Fourteen chevrons were counted during examination of the flensed carcass, but only 13 chevrons were found when the cleaned skeleton was examined (the smallest and last chevron(s) was(were) missing). On each side, there were five double-headed and seven single-headed vertebral ribs (no floating ribs were observed, but loss of small floating ribs could not be precluded; this uncertainty would affect the thoracic and lumbar counts but not the total number of vertebrae) and seven sternal ribs. Three mesosternal elements are fused solidly into a single unit, and the basihyal and thyrohyals are also fused. A small diaphragmatic bone (measuring 40.9 mm long and 5.5 mm wide at about the midpoint of the bone) was also present and found along the midline of the diaphragm and just ventral to the vertebral column (likely an ossification in the central tendon). On vertebrae Ca3 to Ca5, there are osteopathological growths with an especially large (about 5.9 cm long and 3.2 cm wide) mass on the right dorsal posterior surface of Ca4. The seventh right vertebral rib was broken and partially healed with signs of infection, which may have resulted in the bone not healing properly. The skeleton specimen is nearly complete, but the scapulae and teeth were not available when we examined the specimen; the tympanic bones are glued to the skull (likely to the wrong sides). The skeleton is maintained in the collection of the National Museum of Natural Science (NMNS), Taichung City, Taiwan. The dorsal view of the calvaria of the holotype is shown in Figure 6A; other views of its calvaria and bones are available in Additional file 4.

Type locality

The specimen was found stranded on a beach of Tongshiao, Miaoli County (Taiwan) on 25 September 2009. The specimen's condition was fresh (code 2 of Geraci and Lounsbury 2005) and highly emaciated and showed clear signs of net entanglement (around the tail stock, flukes, rostrum, flippers and possibly the dorsal fin) that likely resulted in her death.

Paratypes

NMNS-6366 (=JYW-00-08): An adult of 247.0 cm (total body length) that was found stranded on a beach of

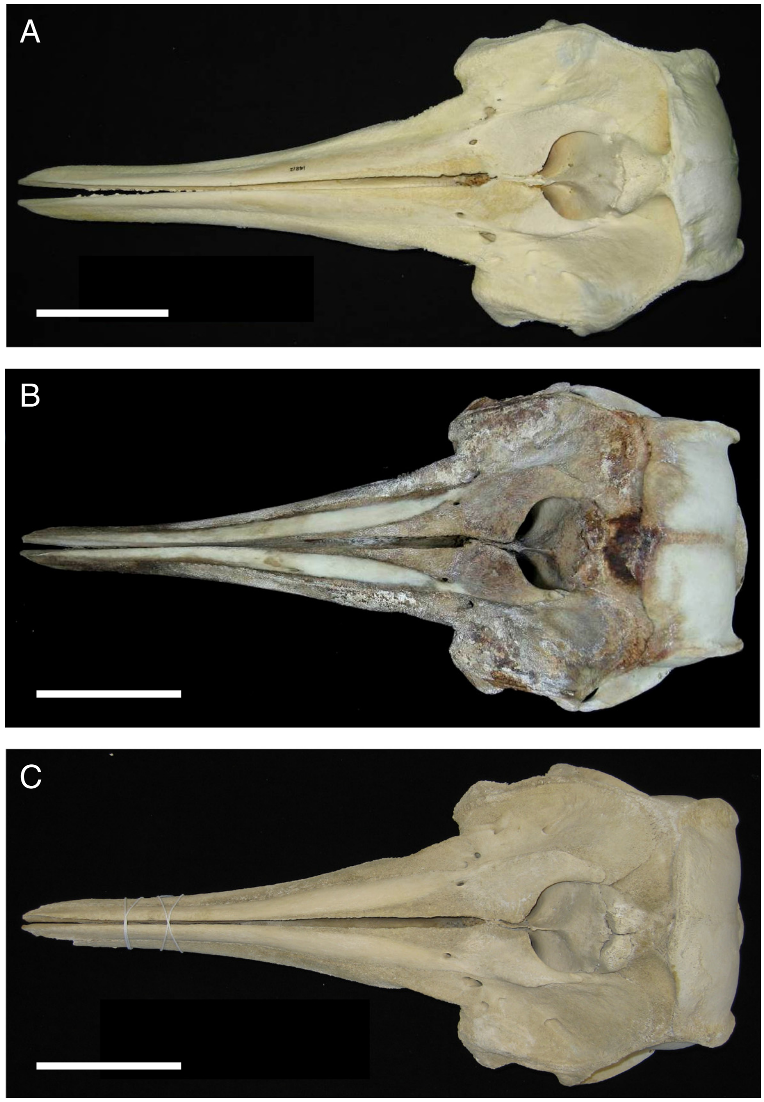

Figure 6 Dorsal views of the calvariae of *Sousa chinensis taiwanensis* specimens. **(A)** holotype (NMNS-14812 (=JYW-09-01)) and paratypes **(B)** NMNS-6366 (=JYW-00-08) and **(C)** TN-2005-35 (=JYW-05-12). The white thick bars represent 10 cm in each photograph. Photographs by J.Y. Wang/*FormosaCetus* Research and Conservation Group.

Tongshiao, Miaoli County (Taiwan) on 8 August 2000. Physically mature. Condylobasal length: 504.5 mm. Vertebral formula: Ce7 + T12 + L9 + Ca24 = 52. This skeleton is also in the collection of the National Museum of Natural Science. The dorsal view of the specimen's calvaria is shown in Figure 6B.

TN-2005-35 (=JYW-05-12): An adult measuring approximately 250 cm (total body length) that was found stranded on a beach near Chigu, Tainan County (Taiwan) on 24 April 2005. Physically mature. Condylobasal length: 496.0 mm. Vertebral formula: Ce7 + T12 + L + Ca33 = 52. The specimen is maintained at the interpretation centre of the Si-Cao Protected Area, Tainan County, Taiwan. The dorsal view of the calvaria is shown in Figure 6C.

More details about these paratype specimens are available in Additional file 5.

Etymology

The proposed subspecies name reflects the endemic distribution of the subspecies in the waters of western Taiwan and in the same flavour as other endemic subspecies of Taiwan. Similar to the common names for *S. c. chinensis*, we suggest Taiwanese humpback dolphin or Taiwanese white dolphin, which is the direct translation of a local common name, 'Taiwan bai hai tun'.

Diagnosis

The general overall pigmentation and the complex developmental changes that occur are similar to those of

S. c. chinensis. Young calves and juveniles (those possessing mostly grey pigmentation with little to no spotting) appear to be indistinguishable from those of *S. c. chinensis*. For older individuals of this subspecies, clear but subtle differences exist. Unlike those of the Pearl River Estuary and Jiulong River Estuary, spotting intensity on the dorsal fin of the Taiwanese subspecies is generally equal to or greater than that on the area of the body adjacent to the dorsal fin (Figure 5D). Thus, the overall colouration of the dorsal fin usually appears to be a smooth continuation of the body or is slightly darker in appearance (of 46 Taiwanese specimens examined, only 2 had dorsal fins that were less spotted than their bodies and then only slightly so). This is the opposite pattern found on *S. c. chinensis* from the Pearl River Estuary and Jiulong River Estuary. However, individuals that are heavily scarred by conspecific aggression (e.g. biting) may exhibit dorsal fins that appear less spotted due to depigmented scarred areas. It is also very rare for Taiwanese dolphins to have little to no spotting on the body, and none documented had an unspotted dorsal fin (Figure 5B).

Distribution

This subspecies is endemic to the shallow coastal waters of central western Taiwan (=eastern Taiwan Strait) including the waters of Miaoli, Taichung, Chunghua, Yunlin, Chiayi and Tainan counties. Dolphins have been reported from as far north as the waters influenced by the Zhonggang and Houlong rivers and south to the waters influenced by the Tzengwen River (near Chigu, Tainan County). With the exception of the intertidal waters inshore of large sandbars of Changhua County, they are generally found less than 3 km from the shore, in waters <30 m deep, and tend to be more commonly observed in and near estuaries (Dares et al. 2014). The known area occupied by this subspecies is about 600 km^2, but the full distribution is likely larger, extending potentially further north to the influences of the Danshuei River Estuary, where suitable habitat appears to be present (Wang et al. 2007a; Ross et al. 2010).

Additional files

Additional file 1: Results from repeating the analyses of Wang et al. (2008a)) on an expanded dataset. Tables of basic descriptive statistics and results of *t*-tests and ANOVAs.

Additional file 2: Data and summary statistics for standard cranial characters and post-cranial meristics. Table of osteological data from specimens of Indo-Pacific humpback dolphins for comparison.

Additional file 3: Invalidity of the proposed neotype of *Sousa chinensis*. Detailed discussion about the invalidity of the neotype specimen for *Sousa chinensis* that was proposed by Porter (2002).

Additional file 4: Additional photographs of the holotype skeleton for *Sousa chinensis taiwanensis*, NMNS-14812 (=JYW-09-01). Photographs of different views of various bones of the holotype.

Additional file 5: Additional details about the paratype specimens of *Sousa chinensis taiwanensis*. More information about the two designated paratype specimens for the new subspecies: NMNS-6366 (=JYW-00-08), TN-2005-35 (=JYW-05-12).

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JYW developed the design of the study, conducted the analyses, drafted the manuscript and obtained funding for and undertook the field work that resulted in the data analysed in this study. SCY and SKH also contributed to data collection in the field, initial processing and analyses of the photographs, and scoring of the photographs. They also helped with the logistics, obtained funding for the field work and provided intellectual discussions that helped in the study. All authors read and approved the final manuscript.

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References

Allen GM (1938) The mammals of China and Mongolia. American Museum of Natural History, New York

Amadon D (1949) The seventy-five percent rule for subspecies. Condor 51:251–258

Amano M, Hayano A (2007) Intermingling of *dalli*-type Dall's porpoises into a wintering *truei*-type population off Japan: implications from color patterns. Mar Mamm Sci 23:1–14

Araújo CC, Wang JY, Hung SK, White BN, Brito D (2014) Viability of the critically endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphins *Sousa chinensis*. Endang Species Res 24:263–271

Ayoub NA, McGowen MR, Clark C, Springer MS, Gatesy J (2009) Evolution and phylogenetic utility of the melanocortin-1 receptor gene (MC1R) in Cetartiodactyla. Mol Phylogen Evol 52:550–557

Baker AN, Smith ANH, Pichler FB (2002) Geographical variation in Hector's dolphin: recognition of new subspecies of *Cephalorhynchus hectori*. J Royal Soc NZ 32:713–727

Chen H, Zhai K, Chen J, Chen Y, Wen H, Chen S, Wu Y (2008) A preliminary investigation on genetic diversity of *Sousa chinensis* in the Pearl River Estuary and Xiamen of Chinese waters. J Genet Genom 35:491–497

Chen L, Caballero S, Zhou K, Yang G (2010) Molecular phylogenetics and population structure of *Sousa chinensis* in Chinese waters inferred from mitochondrial control region sequences. Biochem Systemat Ecol 38:897–905

Chou L-S, Chang W-L, Wu Y-J, Yu H-Y (2013) Indo-Pacific humpback dolphins in the waters of Kinman: distribution, habitat usage and population structure. J Nat Park (Taiwan) 23:1–10

Dares LE, Hoffman JM, Yang SC, Wang JY (2014) Habitat characteristics of the critically endangered Taiwanese humpback dolphin (*Sousa chinensis*) population of the eastern Taiwan Strait. Aquat Mamm 40:368–374

de Queiroz K (2007) Species concepts and species delimitation. Syst Biol 56:879–886

Dungan SZ (2011) Comparing the social structures of Indo-Pacific humpback dolphins (*Sousa chinensis*) from the Pearl River Estuary and Eastern Taiwan Strait. Trent University, Dissertation

Dungan SZ, Riehl KN, Wee A, Wang JY (2011) A review of the impacts of anthropogenic activities on the critically endangered eastern Taiwan Strait Indo-Pacific humpback dolphins. J Mar Anim Ecol 4(2):3–9

Dungan SZ, Hung SK, Wang JY, White BN (2012) Two social communities in the Pearl River Estuary population of Indo-Pacific humpback dolphins (*Sousa chinensis*). Can J Zool 90:1031–1043

Dungan SZ, Wang JY, Araújo CC, Yang SC, White BN (2015) Social structure in a critically endangered Indo-Pacific humpback dolphin (*Sousa chinensis*) population. Aquat Conserv Mar Freshw Ecosyst (in press)

Durham B (1994) The distribution and abundance of the humpback dolphin (*Sousa chinensis*) along the Natal coast. Dissertation, University of Natal, South Africa

Flower WH (1870) Description of the skeleton of the Chinese white dolphin (*Delphinus sinensis*, Osbeck). Trans Zool Soc London 7:151–160

Frère CH, Hale PT, Porter L, Cockcroft VG, Dalebout ML (2008) Phylogenetic analysis of mtDNA sequences suggests revision of humpback dolphin (*Sousa* spp.) taxonomy is needed. Mar Freshw Res 59:259–268

Frère CH, Seddon J, Palmer C, Porter L, Parra G (2011) Multiple lines of evidence for an Australasian geographic boundary in the Indo-Pacific humpback dolphin (*Sousa chinensis*): population of species divergence? Conserv Genet 12:1633–1638

Geraci JR, Lounsbury VJ (2005) Marine mammals ashore: a field guide for strandings, 2nd edn. National Aquarium in Baltimore, Baltimore

Haig SM, Beever EA, Chambers SM, Draheim HM, Duggar BD, Dunham S, Elliott-Smith E, Fontaine JB, Keisler DC, Knaus BJ, Lopes IF, Loschl P, Mullins TD, Sheffield LM (2006) Taxonomic considerations in listing subspecies under the U.S. Endangered Species Act. Conserv Biol 20:1584–1594

Heyning JE, Perrin WF (1994) Evidence for two species of common dolphins (genus *Delphinus*) from the eastern North Pacific. Contrib Sci (Los Angeles) 442:1–35

Huang W, Wen Y, Tang Z (1978) Preliminary studies on *Sousa chinensis*. Fudan J (Natural Sciences) 1:105–110

Huang S-L, Chang WL, Karczamarski L (2014) Population trends and vulnerability of humpback dolphins *Sousa chinensis* off the west coast of Taiwan. Endang Species Res 26:147–159

Hung SK (2000) Ranging patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary. University of San Diego, People's Republic of China, Dissertation

Hung SK, Jefferson TA (2004) Ranging patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, People's Republic of China. Aquat Mamm 30:159–174

International Commission on Zoological Nomenclature (ICZN) (1999) International code of zoological nomenclature, 4th edn. The International Trust for Zoological Nomenclature, London

Jan S, Wang J, Chern C-S, Chao S-Y (2002) Seasonal variation of the circulation in the Taiwan Strait. J Mar Systems 35:249–268

Jefferson TA (2000) Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. Wildl Monogr 144:1–65

Jefferson TA, Hung SK (2004) A review of the status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in Chinese waters. Aquat Mamm 30:149–158

Jefferson TA, Karczmarski L (2001) *Sousa chinensis*. Mamm Species 655:1–9

Jefferson TA, Rosenbaum HC (2014) Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia. Mar Mamm Sci 30:1494–1541

Jefferson TA, Van Waerebeek KV (2004) Geographic variation in skull morphology of humpback dolphins (*Sousa* spp.). Aquat Mamm 30:3–17

Jefferson TA, Hung SK, Robertson KM, Archer FI (2012) Life history of the Indo-Pacific humpback dolphin in the Pearl River Estuary, southern China. Mar Mamm Sci 28:84–104

Karczmarski L (1996) Ecological studies of humpback dolphins *Sousa chinensis* in the Algoa Bay region, Eastern Cape. Dissertation, University of Port Elizabeth, South Africa

Lin W, Zhou R, Porter L, Chen J, Wu Y (2010) Evolution of *Sousa chinensis*: a scenario based on mitochondrial DNA study. Molec Phylogenet Evol 57:907–911

Lin W, Chang L, Frère CH, Zhou R, Chen J, Chen X, Wu Y (2012) Differentiated or not? An assessment of current knowledge of genetic structure of *Sousa chinensis* in China. J Exp Mar Biol Ecol 416–417:17–20

Mayr E (1982) Of what use are subspecies? Auk 99:593–595

Mayr E, Ashlock PD (1991) Principles of systematic zoology, 2nd edn. McGraw-Hill, New York

Mendez M, Jefferson TA, Kolokotronis S-O, Krützen M, Parra GJ, Colline T, Minton G, Baldwin R, Berggren P, Särnblad A, Amir OA, Peddemors VM, Karczmarski L, Guissamulo A, Smith B, Sutaria D, Amato G, Rosenbaum HC (2013) Integrating multiple lines of evidence to better understand the evolutionary divergence of humpback dolphins along their entire distribution range: a new dolphin species in Australian waters? Mol Ecol 22:5936–5948

Osbeck P (1765) Reise nach Ostindien und China (English translation 1771). Koppe, Rostok

Patten MA (2010) Null expectations in subspecies diagnosis. Ornithol Monogr 67:35–41

Patten MA, Unitt P (2002) Diagnosability versus mean differences of sage sparrow subspecies. Auk 119:26–35

Perrin WF (1972) Variation and taxonomy of spotted and spinner porpoises (genus *Stenella*) of the eastern tropical Pacific and Hawaii. University of California, Dissertation

Perrin WF (1975) Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. Bull Scripps Inst Oceanogr 21:1–206

Perrin WF (1990) Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc Biol Soc Washington 103:453–463

Perrin WF (2009) Coloration. In: Perrin WF, Würsig B, Thewissen JCM (eds) Encyclopedia of marine mammals. Academic Press, San Diego, pp 236–244

Perrin WF, Mitchell ED, Mead JG, Caldwell DK, Caldwell MC, van Bree PJH, Dawbin WH (1987) Revision of the spotted dolphins. Mar Mamm Sci 3:99–170

Phillimore AB, Owens IPF (2006) Are subspecies useful in evolutionary and conservation biology? Proc Royal Soc London B 273:1049–1053

Pilleri G (1979) Pehr Osbeck (1723–1805) and the discovery of the Chinese white dolphin (*Sousa chinensis* Osbeck, 1765). Investig Cetacea 10:333–334

Polanowski AM, Robinson-Laverick SM, Paton D, Jarmin SN (2012) Variation in the tyrosinase gene associated with a white humpback whale (*Megaptera novaeangliae*). J Heredity 103:130–133

Porter LJ (2002) A redescription of *Sousa chinensis* (Osbeck, 1765) (Mammalia, Delphinidae) and designation of a neotype. Bull Nat Hist Mus Zool (London) 68:27–37

Reeves RR, Perrin WF, Taylor BL, Baker CS, Mesnick SL (2004) Report of the workshop on shortcomings of cetacean taxonomy in relation to the needs of conservation and management, April 30 – May 2, 2004 La Jolla, California. NOAA-TM-NMFS-SWFSC-363, National Oceanic and Atmospheric Administration, La Jolla, California

Reeves RR, Dalebout ML, Jefferson TA, Karczmarski L, Laidre K, O'Corry-Crowe G, Rojas-Bracho L, Secchi ER, Slooten E, Smith BD, Wang JY, Zhou K (2008) *Sousa chinensis* (eastern Taiwan Strait subpopulation). In: IUCN 2014. IUCN Red List of Threatened Species. Version 2014.3 Available via IUCN. www.iucnredlist.org. Accessed 12 March 2015

Remsen JV Jr (2010) Subspecies as a meaningful taxonomic rank in avian classification. Ornithol Monogr 67:62–78

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Robineau D, Goodall RNP, Pichler F, Baker CS (2007) Description of a new subspecies of Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804), inhabiting the coastal waters of the Kerguelen Islands. Mammalia 71:172–180

Rommel S (1990) Osteology of the bottlenose dolphin. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 29–49

Rosenbaum HC, Clapham PJ, Allen J, Nicole-Jenner M, Jenner C, Florez-González L, Urbán RJ, Ladrón GP, Mori K, Yamaguchi M, Baker CS (1995) Geographic variation in central fluke pigmentation of humpback whale *Megaptera novaeangliae* populations worldwide. Mar Ecol Prog Series 124:1–7

Ross GJB, Heinsohn GE, Cockcroft VG (1994) Humpback dolphins, *Sousa chinensis* (Osbeck, 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa teuszii*

(Kukenthal, 1892). In: Ridgway SH, Harrison R (eds) The first book of dolphins, vol 5, Handbook on marine mammals, vol. Academic Press, San Diego, pp 23–42
Ross PS, Dungan SZ, Hung SK, Jefferson TA, MacFarquhar C, Perrin WF, Riehl KN, Slooten E, Tsai J, Wang JY, White BN, Würsig B, Yang SC, Reeves RR (2010) Averting the baiji syndrome: conserving habitat for critically endangered dolphins in Eastern Taiwan Strait. Aquat Conserv Mar Freshw Ecosyst 20:685–694
Ryder OA (1986) Species conservation and systematics: the dilemma of subspecies. Trends Ecol Evol 1:9–10
Schaeff CM, Hamilton PK (1999) Genetic basis and evolutionary significance of ventral skin color markings in North Atlantic right whales (*Eubalaena glacialis*). Mar Mamm Sci 15:701–711
Slooten E, Wang JY, Dungan SZ, Forney KA, Hung SK, Jefferson TA, Riehl KN, Rojas-Bracho L, Ross PS, Wee A, Winker R, Yang S-C, Chen CA (2013) Impacts of fisheries on the critically endangered humpback dolphin *Sousa chinensis* population in the eastern Taiwan Strait. Endang Species Res 22:99–114
Taxonomy Committee of the Society for Marine Mammalogy (2014) List of marine mammal species and subspecies. http://www.marinemammalscience.org/species-information/list-of-marine-mammal-species-subspecies/. Accessed 12 March 2015
Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems, and time durations. J Biogeogr 27:1153–1167
Wang P (1999) Chinese cetaceans. Ocean Enterprises Limited, Hong Kong Special Administrative Region
Wang P, Han J (1996) On the Chinese white dolphin found in the Xijiang River and the mouth of the Yangtze River and its status of resource distribution. Aquat Products Sci 15:3–8
Wang P, Sun J (1982) Studies on the Zhonghua white dolphin, *Sousa chinensis*, from the South China Sea. Trans Liaoning Zool Soc 3:67–76
Wang JY, Yang SC (2007) An identification guide to the dolphins and other small cetaceans of Taiwan. Jen Jen Publishing Company and National Museum of Marine Biology and Aquarium, Taiwan
Wang JY, Yang SC (2011) Evidence for year-round occurrence of the eastern Taiwan Strait Indo-Pacific humpback dolphins (*Sousa chinensis*) in the waters off western Taiwan. Mar Mamm Sci 27:625–658
Wang JY, Hung SK, Yang S-C (2004a) Records of Indo-Pacific humpback dolphins, *Sousa chinensis* (Osbeck, 1765), from the waters of western Taiwan. Aquat Mamm 30:187–194
Wang JY, Yang SC, Reeves RR (eds) (2004b) Report of the first workshop on conservation and research needs of Indo-Pacific humpback dolphins, *Sousa chinensis*, in the waters of Taiwan, February 2004. National Museum of Marine Biology and Aquarium, Checheng
Wang JY, Yang SC, Hung SK, Jefferson TA (2007) Distribution, abundance and conservation status of the eastern Taiwan Strait population of Indo-Pacific humpback dolphins, *Sousa chinensis*. Mammalia 71:157–165
Wang JY, Hung SK, Yang SC, Jefferson TA, Secchi ER (2008a) Population differences in the pigmentation of Indo-Pacific humpback dolphins, *Sousa chinensis*, in Chinese waters. Mammalia 72:302–308
Wang JY, Frasier TR, Yang SC, White BN (2008b) Detecting recent speciation events: the case of the finless porpoise (genus *Neophocaena*). Heredity 101:145–155
Wang JY, Yang SC, Fruet PF, Secchi ER (2012) Mark-recapture analyses of the critically endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphins (*Sousa chinensis*): implications for conservation. Bull Mar Sci 88:885–902
Zhou K (2004) Fauna sinica mammals volume 9 Cetacea, Phocoidea, Sirenia. Science Press, Beijing, Carnivora
Zhou K, Leatherwood S, Jefferson TA (1995) Records of small cetaceans in Chinese waters: a review. Asian Mar Biol 12:119–139
Zink RM (2004) The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proc Royal Soc London B 271:561–564