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Abstract

The taxonomy of dolphins within the genus *Tursiops* is controversial. Although two species, the common bottlenose dolphin, *T. truncatus,* and the Indo-Pacific bottlenose dolphin, *T. aduncus*, are currently recognized, additional taxonomic units have been suggested. Within *T. aduncus*, populations occurring along the eastern African coast are genetically different from populations in the western Pacific. To clarify the phylogeographic affinity of Indo-Pacific bottlenose dolphins from Bangladesh, sequences from the mitochondrial DNA control region were obtained and an analysis including previously published sequences of *T. aduncus* was conducted. High levels of genetic differentiation were found among three distinct clusters identified in the phylogenetic analyses for *T. aduncus* in Bangladesh; along the eastern African coast; and from China, Australia, Indonesia and Melanesia. The levels of differentiation are within the ranges reported for other dolphin species. These results show that bottlenose dolphins occurring off Bangladesh are genetically distinct from *T. aduncus* occurring to the east and west. This suggests that they potentially are a different phylogenetic unit. Additional information from morphological and molecular characters are needed to clarify their taxonomic status.

Introduction

The taxonomy and systematics of the *Tursiops* genus are controversial. Two species are currently recognized: the common bottlenose dolphin, *Tursiops truncatus*, and the Indo-Pacific bottlenose dolphin, *T. aduncus* (LeDuc *et al.* 1999). *T. aduncus* is distributed in coastal waters of Indian and western Pacific Oceans, although the continuity of its distribution is unknown (Wang and Yang 2009). Although it has not been formally recognized (Committee on Taxonomy, 2014), a third species, *T. australis*, was recently named from Southern Australia, based on distinct morphological and genetic characters (Charlton-Robb *et al.* 2011; Möller *et al.* 2008).

The genus *Tursiops* has been found to be polyphyletic in some phylogenetic studies of the subfamily Delphininae, particularly those analysing mitochondrial DNA regions (e.g. Amaral *et al.* 2012; Kingston *et al.* 2009; LeDuc *et al.* 1999; Möller *et al.* 2008)

while some other studies, based on nuclear DNA regions found support for monophyly (e.g. Amaral *et al.* 2012; McGowen 2011; Steeman *et al.* 2009).

Within *T. aduncus*, there is strong genetic differentiation between populations occurring along the coast of Africa and populations occurring in the Indo-West Pacific region. (China, Japan, Korea, Melanesia, Australia). Wang *et al*. (1999) examined mtDNA control region sequences from *Tursiops* sampled in Taiwanese waters and concluded there were two species (*T. truncatus*, *T. aduncus*). Möller and Beheregaray (2001) concluded based on genetic samples from coastal *Tursiops* from southeastern Australia (Jervis Bay and Port Stephens) that both were *T. aduncus*, but these sequences were not compared with ones from South Africa. Natoli *et al*. (2004), using mtDNA and microsatellite markers, found that coastal *T. aduncus* in South Africa differed significantly from both *T. aduncus* from Taiwan and *T. truncatus* from various locations worldwide (Atlantic, Gulf of Mexico, Mediterranean Sea and the eastern North Pacific). Therefore, they concluded that the *T. aduncus* in Taiwan may represent a third species. However, Natoli and colleagues did not examine any sequences from Australia *T. aduncus*. Kemper (2004) examined skulls and skeletons of mature bottlenose dolphins from mainly southern Australia and determined that they could be assigned to either *T. truncatus* or *T. aduncus* based on morphology, but no genetic sequences from these specimens were analyzed. However, all of this leads to the proposition that the two forms found in the Indo-Pacific constitute different taxonomic units, species or subspecies. (Natoli *et al.* 2004; Sarnblad *et al.* 2011; Wang *et al.* 1999; Oremus *et al.* 2015). Genetic analysis of the holotype specimen of *T. aduncus* from the Red Sea shows that it groups with the African form. The taxonomy of Indo-Pacific bottlenose dolphins therefore requires major revision Here we follow Oremus *et al.* 2015 by referring to these two forms as the "African" *T. aduncus* and the "Pacific" *T. aduncus*.

Little information is available on the population structure of Indo-Pacific bottlenose dolphins at smaller scales even through it has been suggested that the species is composed by many small, localized populations that are fairly isolated from each other. Sarnblad *et al*. 2011 found genetic differences between dolphins occurring in Northern and Southern Zanzibar, suggesting that differentiation may arise even across small geographic scales. Similar results were obtained with *T. aduncus* occurring in Melanesia, where evidence of population structure was found between the Solomon Islands and New Caledonia (Oremus *et al*. 2015).

The waters at the head of Swatch-of-No-Ground (SoNG) submarine canyon in Bangladesh support one of the world's largest populations of Indo-Pacific bottlenose dolphins (Mansur *et al.* 2012). However, the survival of these dolphins is potentially threatened by interactions with fisheries since their distribution highly overlaps with operating gill net fisheries and a large portion (28.2%) of individuals identified from dorsal fin photographs exhibited injuries related to entanglements in fishing gear (Mansur *et al*. 2012). It is therefore important to assess not only the genetic diversity of this population, but also their genetic 'affinity' and taxonomic relationship with neighbouring populations.

This study aims to identify the phylogeographic affinity of Indo-Pacific bottlenose dolphins occurring in the northern Bay of Bengal, Bangladesh. For this, we sequenced a fragment of the mitochondrial DNA control region. Comparisons with published

sequences available in GenBank of *T. aduncus* from South Africa (Natoli *et al*. 2004); Zanzibar (Sarnblad *et al*. 2011); India and Australia (Möller *et al.* 2001); Indonesia, and China (Wang *et al*. 2009); and Melanesia (Oremus *et al*. 2015) were made.

Material and Methods

Sampling

In total, 17 Indo-Pacific bottlenose dolphin samples from Bangladesh were included in this study. A single tooth was obtained from a mandible collected in the Andaman Islands (eastern part of the Bay of Bengal) in 1889. This mandible (3406) is part of the collection of the Natural History Museum of the University of Florence, Italy. In order to include these newly generated sequences in a broad phylogeographic analyses of *T. aduncus*, sequences encompassing different geographical regions corresponding to the putative "African" *T. aduncus* and "Pacific" *T. aduncus* were retrieved from GenBank (Table 1).

Laboratory procedures

Genomic DNA was extracted using from tissue samples using the QIAamp Tissue Kit (QIAGEN, Valencia, CA, USA). A fragment of the mitochondrial DNA control region was amplified and sequenced (Baker *et al*. 1993). The PCR profile consisted of an initial denaturation for 3 min at 94ºC followed by 32 amplification cycles (30s at 94ºC, 30s at 52º, 1 min at 72ºC) and a final 5 min of extension at 72ºC. Both strands were directly sequenced (BigDye Terminator CycleSequencing; Applied Biosystems) on an ABI 3730 automated sequencer (Applied Biosystems).

Table 1. Indo-Pacific bottlenose dolphin mitochondrial DNA control region sequences retrieved from GenBank.

Species	Region	GenBank	Reference
"African" *T. aduncus*	Zanzibar	HM104224 - HM104229	Sarnblad et al. 2011
	South Africa	EF636207-EF632212	Natoli et al. 2004
	Red Sea (Holotype)	DQ517442	Perrin et al. 2007
"Pacific" *T. aduncus*	Melanesia	KF555572-KF555571	Oremus et al. 2015
	Australia	JX183247-JX183258	Ansmann et al. 2012
	Australia	AF287951-AF287955	Möller and Beheregaray 2001
	Australia	EF581128	Möller et al. 2008
	Australia	KJ530735-KJ530740	Brown et al. 2014
	Australia	GQ420670/HQ115064	Wiszniewski et al. 2010
	China / Taiwan	AF056233-AF056237 / AF056240-AF056243	Wang et al. 1999
	Indonesia	AF056238-AF056239	Wang et al. 1999
	China	AF355576-AF355581	Ji et al. 2001 unpublished
	China	HQ436290-HQ436299	Zhang 2011 unpublished
	China	AF459506-AF459523	Ji et al. 2002 unpublished

Statistical analyses

DNA sequences were inspected, edited and aligned by eye in Sequencher 5.0.1 (Gene Codes, Corp.). Sequences were collapsed into haplotypes using DNAsp v. 5.10 (Librado and Rozas 2009). Diversity measures (nucleotide and haplotype diversities and the average number of nucleotide differences) were also estimated in DNAsp for the Bangladesh population. In order to assess the degree of genetic differentiation between the Bangladesh dolphins and the other *T. aduncus* groups, the net average, d_A, and the mean gross, d_{xy}, distances were estimated in the software MEGA v. 6. With 5000 bootstrap replicates (Tamura *et al.* 2013). The best model of nucleotide substitution for the dataset was determined using the Akaike Information Criterion (AIC) as implemented in the program Modeltest v. 2.1.7 (Darriba *et al.* 2012; Guindon and Gascuel 2003). The model selected was HKY with a proportion of invariable sites and a gamma-shaped distribution of rates across sites (G=0.429). This model was therefore used to calculate d_A and d_{xy}.

A median-joining network of all haplotypes was constructed in NETWORK v. (Bandelt *et al.* 1999). A phylogenetic tree was estimated in MEGA v. 6. using the Maximum-Likelihood (ML) method, with the HKY model as the nucleotide substitution model and the Nearest-Neighbor-Interchange Heuristic method with Branch Swap Filter. One thousand bootstrap replicates were run to assess robustness of the phylogeny estimated. A sequence of the rough-toothed dolphin, *Steno bredanensis*, was used as outgroup.

Results

In total, 380 bp of the mitochondrial DNA control region were sequenced and analysed. The 17 sequences obtained for the Bangladesh bottlenose dolphins grouped into 8 haplotypes. Genetic diversity measures were within the range that has been described for other *T. aduncus* populations. The estimated haplotypic diversity (0.699 ±0.117) is relatively low, but similar to values obtained for South Africa, Zanzibar and Australia populations (Sarnblad *et al.* 2011). Conversely, the estimated nucleotide diversity (0.009 ±0.005) is relatively high and similar to values obtained for China/Taiwan and the Solomon Islands populations (Oremus *et al.* 2015).

The net average, d_A and the mean gross, $d_{xy,}$ genetic divergence estimates between the different groups included in this study show a high level of differentiation between the Bangladesh *T. aduncus* population and all others (Table 2). Values for d_A varied between 0.05 and 0.08 and d_{xy} values varied between 0.06 and 0.09. Values of the same order of magnitude were also obtained in comparisons between "African" and "Pacific" *T. aduncus,* suggesting that the three bottlenose dolphins groups are genetically divergent. Comparisons between the different populations within the "Pacific" *T. aduncus* group showed much lower levels of divergence (Table 2).

Table 2. Net divergence (*d*A, below diagonal) and mean gross divergence (*d*x,y, above diagonal) estimated between the different *T. aduncus* geographical regions. All values were statistically significant ($P<0.05$). EAFR – East Africa; BAN – Bangladesh; IND – Indonesia; CH – China; MEL – Melanesia; and AUS – Australia. Grey area highlights comparisons within "Pacific" *T. aduncus* populations.

		African *T. aduncus*		Pacific *T. aduncus*			
		EAFR	BAN	IND	CH	MEL	AUS
African *T. aduncus*	EAFR		0.064	0.079	0.058	0.062	0.062
	BAN	0.052		0.095	0.079	0.080	0.083
Pacific *T. aduncus*	IND	0.065	0.080		0.026	0.020	0.028
	CH	0.042	0.063	0.007		0.018	0.025
	MEL	0.050	0.068	0.005	0.002		0.023
	AUST	0.043	0.063	0.005	0.001	0.003	

The haplotype network and phylogenetic tree also showed the presence of three distinct clusters: one corresponding to the Bangladesh *T. aduncus* (including the the Andaman Islands specimen) and the other two to the "African" and "Pacific" *T. aduncus*. There were no shared haplotypes among these three groups (Figure 1). The only shared haplotypes were within the "Pacific" *T. aduncus* haplogroup. One haplotype was shared between China and Australia, one shared between Melanesia and Australia and the other one shared between Indonesia and China. The complex relationships obtained in the "Pacific" *T. aduncus* haplogroup suggest that there is gene flow between the different geographical regions analysed in China, Australia, Indonesia and Melanesia, as also suggested by low genetic divergence values obtained. There was one haplotype from Bangladesh that grouped with the "Pacific" *T. aduncus*" group. The holotype specimen grouped with the "African" *T. aduncus* sequences.

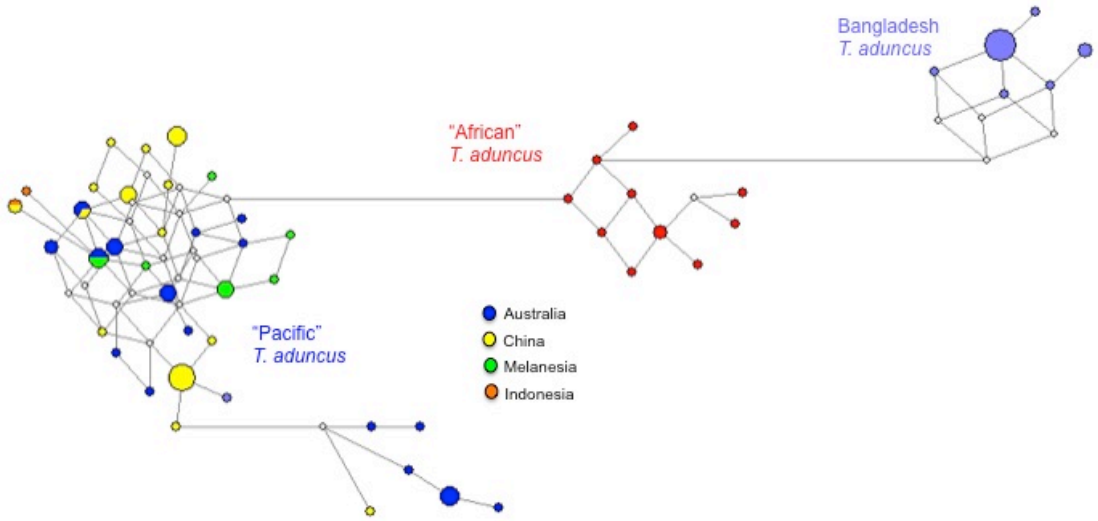

Figure 1. Median-joining haplotype network of the mitochondrial control region sequences. Circle size is proportional to the number of individuals exhibiting the corresponding haplotype and proportional of each population within each haplotype is coloured according to the legend. Length of lines is proportional to the number of mutational steps separating haplotypes. White circles indicate missing intermediate haplotypes.

In the Maximum-likelihood phylogenetic tree, although there was no resolution of the sister taxa relationship among the three main clusters, a high bootstrap value was found to support the distinction of the Bangladesh *T. aduncus* cluster (Figure 2).

The alignment of the haplotype sequences displaying the variable sites clearly shows the differences in polymorphisms between the three groups mentioned above (Figure 3). There are 5 fixed nucleotide differences that can diagnose all Bangladesh sequences (with the haplotype from the Andaman Islands included) from "Pacific" and "African" *T. aduncus*, with the exception of one haplotype, which is the one that clustered with the "Pacific" *T. aduncus* samples in the haplotype network and phylogenetic tree. Conversely, only two fixed nucleotide differences can diagnose all "African" *T. aduncus* sequences.

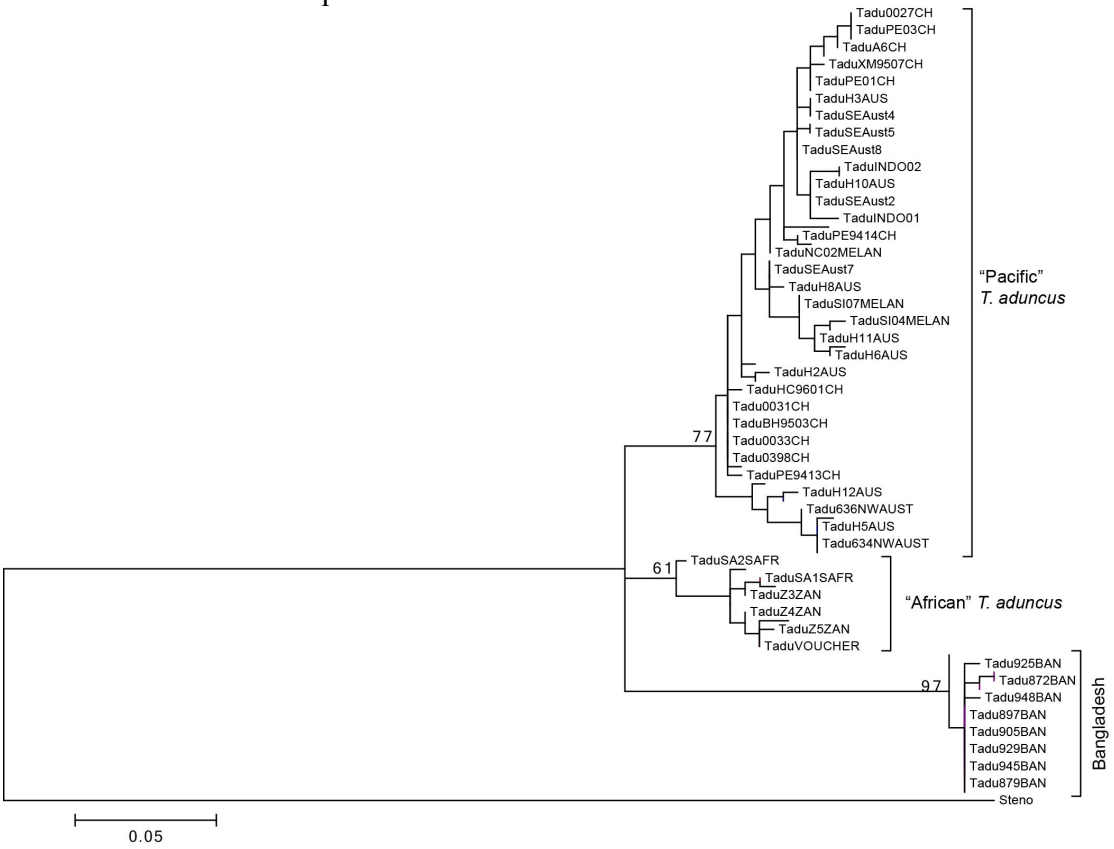

Figure 2. Maximum-likelihood phylogenetic tree obtained for the mitochondrial DNA control regions sequences of *T. aduncus*. Values above branches correspond to bootstrap support values.

Discussion

In this study we analysed sequences from the mitochondrial DNA control region of Indo-Pacific bottlenose dolphins, *T. aduncus,* obtained across its distribution, with the aim of assessing the phylogeographic affinity of dolphins occurring in the northern Bay of Bengal, Bangladesh. The results suggest that bottlenose dolphins from this region are predominantly highly genetically different from the two forms occurring along the eastern African coast ("African" *T. aduncus*) and to the west ("Pacific" *T. aduncus*). The level of differentiation for the Bangladesh population suggests significant reproductive isolation among all three populations and that they constitute different phylogenetic units, as has been previously suggested for the African and

Pacific forms (Natoli *et al*. 2004; Sarnblad *et al*. 2011). Information from additional molecular markers from the nuclear genome or morphological characters (Reeves et al. 2004), are needed in order to determine the degree the taxonomic identity of the Bangladesh form.

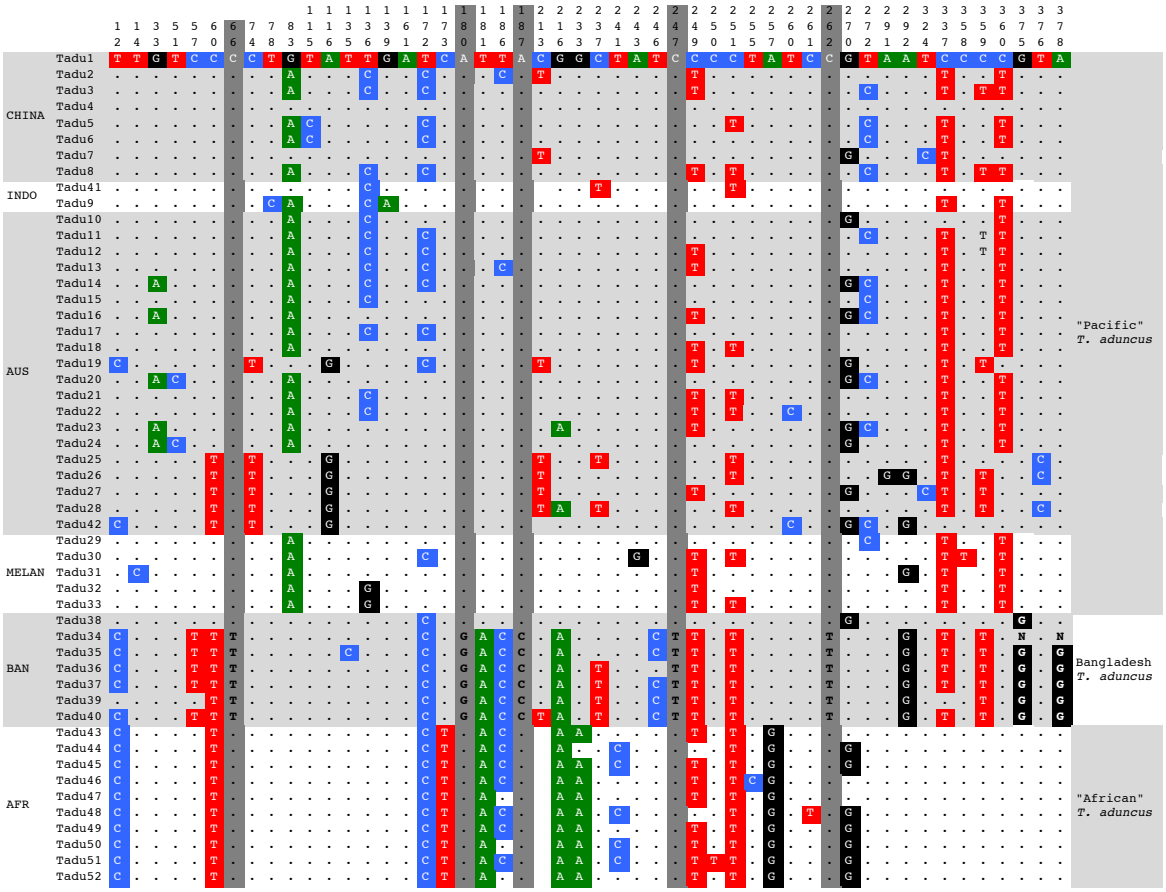

Figure 3. Character matrix depicting the mitochondrial control region polymorphisms that define the different *T. aduncus* haplotypes. Fixed nucleotide positions diagnostic of Bangladesh sequences are highlighted in dark grey.

The Bangladesh dolphins showed a relatively low level of haplotype diversity, but a high level of nucleotide diversity. This is consistent with what has been previously described for *T. aduncus* populations throughout their distribution (Natoli *et al*. 2004; Sarnblad *et al*. 2011; Oremus *et al.* 2015). The fact that these dolphins form small, isolated populations can lead to lower levels of genetic diversity when compared to other more oceanic species like the common bottlenose dolphin, *T. truncatus*. A lower haplotype diversity and higher nucleotide diversity can also indicate either a bottleneck or a founder event in the population where haplotypes have been lost. The data analysed in this study do not allow for the distinction between these different scenarios. However, the localized occurrence of the bottlenose dolphins in Bangladesh straddling fairly shallow (19m) to deep-water (>200m) habitat about 30 km offshore at the head of the SoNG and their absence in shallow water closer to shore (Smith, unpublished), the latter of which is more typical of habitat in the range of *T. aduncus* (Wang 2009), imply that the concentrated productivity created by upwelling currents found along the canyon edge may have promoted reproductive isolation.

The level of genetic differentiation and the number of fixed nucleotide substitutions separating Bangladesh dolphins from the "African" and "Pacific" forms of *T. aduncus* is similar to the levels differentiating other dolphin species within polytypic genera such as *Sousa* (Mendez *et al*. 2013) in the Indo-Pacific. It is also noteworthy that a recent analysis of humpback dolphins from Bangladesh found that are also distinct from other members of the *Sousa* genus occurring in the Pacific and along the African coast (Amaral *et al.* 2015) potentially suggesting a more general mechanism promoting reproductive isolation of mobile marine species in the northern Bay of Bengal.

The genetic uniqueness of these dolphins must be taken into consideration when designing and implementing conservation plans, since gene flow with neighbouring *T. aduncus* populations is unlikely. There was one haplotype from Bangladesh that clustered with the "Pacific" *T. aduncus* haplotypes, which may be the result of ancestral polymorphism or convergence.

Although the phylogenetic tree of mtDNA control region sequences obtained could not resolve the sister taxa relationship among the three different clusters, the Bangladesh *T. aduncus* seem to be more closely related to the "African" *T. aduncus* than to the "Pacific" *T. aduncus*. The lower level of genetic differentiation obtained by d_A and d_{xy} values and the higher number of shared polymorphisms support this finding.

The specimen from the Andaman Islands clustered with Bangladesh *T. aduncus* suggesting that Indo-Pacific bottlenose dolphins occurring in the northern and eastern Bay of Bengal may be genetically very similar, but different from other *T. aduncus*. Research is needed on the morphology of these Bangladesh *Tursiops* to clarify their relationships to those populations to their east and west.

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Notes

There is one nominal species of *Tursiops* from the region (India) with an existing holotype and it is *Tursiops fergusoni* Lydekker, 1903 from Trivandrum (8° 29′ 15″ N, 76° 57′ 9″ E) and the holotype was deposited in the British Museum (Natural History).

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