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Cranial Variation and Taxonomic Revision of Bottlenose Dolphins (*Tursiops* spp.) from Japanese Waters

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Abstract

We analyzed the skulls of 27 bottlenose dolphins (*Tursiops* spp.) from the waters around Japan to clarify their systematics. We divided the Japanese bottlenose dolphins into two morphological groups. Group A was comprised of six specimens from the coastal waters of the Amami Islands, Amakusa-Shimoshima Island, and Mikura Island. Group B included 21 specimens from other waters around Japan. Comparisons with type specimens showed that Groups A and B were identical to the types of *T. aduncus* and *T. truncatus*, respectively. These results support previous molecular studies on some specimens identified as *T. aduncus*.

Key Words: *Tursiops aduncus*, *Tursiops truncatus,* bottlenose dolphin, Japanese waters, morphology, taxonomy

Introduction

Bottlenose dolphins (*Tursiops truncatus*, Montagu, 1821) have a worldwide distribution in tropical to temperate coastal waters. Because dolphins exhibit high morphological variation (Turner & Worthy, 2003), many species of bottlenose dolphin have been described—for example, *T. aduncus* (Ehrenberg, 1832), *T. cymodoce* (Gray, 1846), *T. catalania* (Gray, 1862), *T. gilli* (Dall, 1873), and *T. gephyreus* (Lahille, 1908). Most of these species are no longer recognized, however, and two main species have been identified within this genus: *T. truncatus* and *T. aduncus* (or *T. cf. aduncus*) (van Bree, 1966; Ross, 1977; Gao et al., 1995; Wang et al., 1999, 2000a; Hale et al., 2000). Van Bree (1966) distinguished the *Tursiops* spp. in the coastal waters of West Africa into *T. aduncus* and *T. truncatus* using rostrum length. Ross (1977) suggested that the two species were sympatric in South African waters and mainly distinguished by the ventral spotting in adult *T. aduncus* and absence of spotting in *T. truncatus*. Wang et al. (2000a) described a longer rostrum and smaller body size in *T. truncatus* in Chinese waters. LeDuc et al. (1999) distinguished *T. aduncus* from *T. truncatus* using mitochondrial DNA analysis. The assignment of these two species is sometimes unclear (Rice, 1998), however, because of the large geographical variation in this genus and the lack of worldwide studies. Ross & Cockcroft (1990) stated that the morphology of bottlenose dolphins in Australian waters is gradually variable. Hershkovitz (1966) described *T. aduncus* as a subspecies of *T. truncatus*, and some authors recognize only a single species, *T. truncatus* (Tomilin, 1962; Jefferson et al., 1993; Mead & Brownell, 1993). In addition, True (1914) noted that few data are available for the *T. aduncus* type. Thus, the taxonomical relationship between *T. truncatus* and *T. aduncus* is unclear at the global level, and local studies and examinations of type specimens are needed.

In Japanese waters, bottlenose dolphins without ventral spotting (*truncatus* type) are common (Kasuya et al., 1997). In contrast, spotted bottlenose dolphins (*aduncus* type) have been reported from the coastal waters of the Amami Islands, Amakusa-Shimoshima Island, the Bonin Islands (also known as the Ogasawara Islands), and Mikura Island (Miyazaki & Nakayama, 1989; Kasuya et al., 1997; Kakuda et al., 2002; Shirakihara et al., 2003). Kakuda et al. (2002) implied that specimens from the Mikura waters resemble *T. aduncus* from Chinese waters (Wang et al., 1999, 2000a, 2000b) or South African waters (van Bree, 1966; Ross, 1977). Shirakihara et al. (2003) also suggested that bottlenose dolphins from Amakusa-Shimoshima Island were similar to *T. aduncus* described by Ross (1977). Bottlenose dolphins from Japanese waters have yet to be fully investigated, however. Thus, we analyzed the skulls of bottlenose dolphins from Japanese waters and compared the type skulls of *T. truncatus* and *T. aduncus* to discuss the taxonomic position of bottlenose dolphins from Japanese waters.

Materials and Methods

We examined the skulls of 27 bottlenose dolphins (*Tursiops* spp.) from Japanese waters: 23 skulls from the National Science Museum in Tokyo, Japan; two from the Kumamoto City Museum in Kumamoto, Japan; and one each from the private collection of Amakusa Iruka World, Kumamoto, Japan, and the Experimental Station of Highland Animal Production at Nagoya University. Of these 27 specimens, four (NSMT30133, NSMT32733, KCM-01-000159, and KCM-01-000160) were already reported to be from a different clade than *truncatus*-type specimens using mitochondrial DNA analysis (Kakuda et al., 2002; Shirakihara et al., 2003). We also examined the skulls of type specimens of *T. truncatus* and *T. aduncus* for comparison with Japanese bottlenose dolphins. The type specimen of *T. truncatus* was described by Montagu (1821; type locality: Dunncanon Pool, Devonshire, UK) and was located at the Natural History Museum, London, UK (NHM353a). The type specimen of *T. aduncus*, which was identified as the holotype by van Bree in 1978 (type locality: Belhosse Island, Red Sea), was located at the Museum fur Naturkunde, Berlin, Germany (ZMB6640). See Figure 1 and Appendix 1 for details of the specimens.

Thirty-one skull metric character points were measured on the left side of the skull to the nearest 0.05 mm using calipers (Figure 2). All measurements were based on Perrin (1975), Wang et al. (2000a), and Kakuda et al. (2002), and included condylobasal length (CBL), greatest length of the left pterygoid (GLP), greatest length of the left temporal fossa (GLTF), greatest postorbital width (GPOW), greatest preorbital width (GPRW), greatest parietal width within the postotemporal fossa (GPWPF), greatest width of the external nares (GWEN), greatest width of the internal nares (GWIN), greatest width of the premaxillaries (GWP), greatest width of the left temporal fossa (GWTF), length of the antorbital process of the lachrymal (LAL), least supraorbital width (LSW), lower tooth row length to tip of rostrum (LTRL), mandibular fossa length (MFL), mandible height (MH), mandible length (ML), minimum width of the pterygo-palatine complex (MWPP), number of teeth on the lower left (NTL), number of teeth on the upper left (NTU), premaxillary width at mid-length (PWM), rostrum length (RL), rostrum width at base (RWB), rostrum width at mid-length (RWM), rostrum width at one-quarter distance from the posterior end (RW1/4), rostrum width at three-quarters distance from the posterior end (RW3/4), tip of the rostrum to external nares (TREN), tip of the rostrum to internal nares (TRIN), upper tooth row length to the tip of the rostrum (UTRL), width of the alisphenoid at the basisphenoid suture width (BSW), zygomatic width of premaxillaries (ZW), and the tip of the rostrum to the apex of the premaxillary convexity (TPC). TPC was defined as the point of intersection between both ridges from the antorbital notch.

We used principal component analysis (PCA; *SPSS*, *Version 13.0*, SPSS Inc., Chicago, IL) to determine whether bottlenose dolphins from Japanese waters belong to two or more morphological groups. Because the analysis is

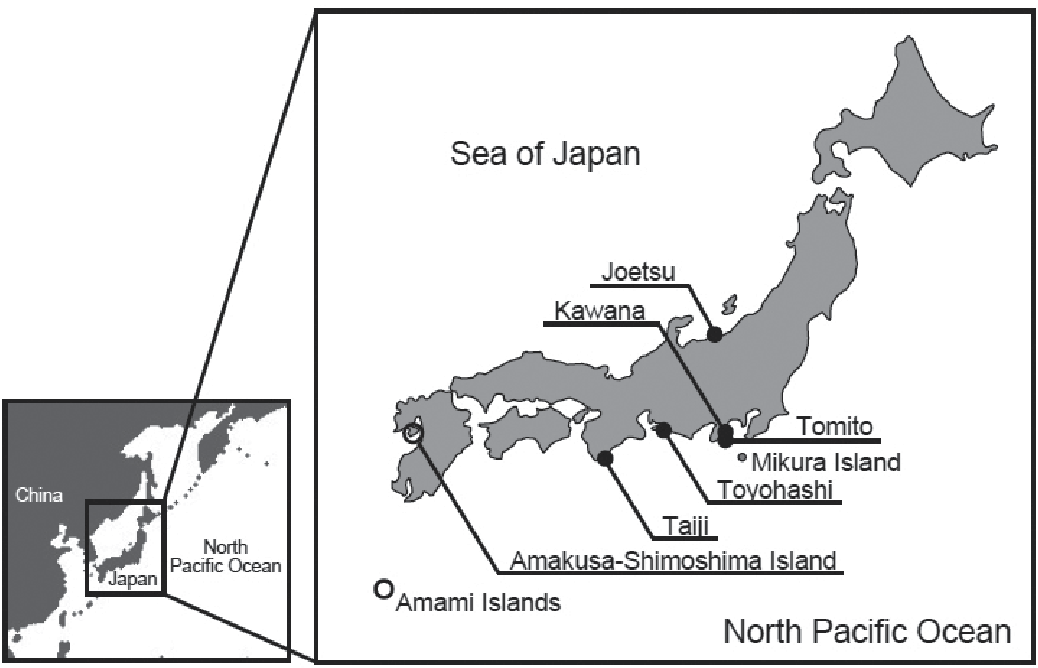

Figure 1. Collection locations for *Tursiops* spp. in Japanese waters

sensitive to missing data, we used 25 selected characters for the analysis. ANCOVA was performed on characters correlated with the CBL measurement to avoid ontogenetic variation and to analyze algometric growth (*StatView*, *Version 5*, SAS Institute, Cary, NC). Mann-Whitney U-tests were performed on characters not correlated with CBL (*StatView*, *Version 5*).

MANOVA (Wilks' likelihood-ratio method; *StatView*, *Version 5*) was performed to test for differences between sexes ($F = 9.831$, $p > 0.05$). Because no significant differences were observed between sexes, they were combined for further analysis.

Results

Morphological Groups Within Bottlenose Dolphins from Japanese Waters

Two principal components (PC1 and PC2) were extracted in the PCA on the data matrix of the 27 *Tursiops* spp. from Japanese waters (Table 1). The cumulative variance explained by PC1 and PC2 was 89.27% (76.12 and 13.14%, respectively). PC1 was strongly affected by all measurements except TPC. The specimens KCM-01-000159, NSMT28346, and NMST27003 were separated from the other specimens (Figure 3) because they were much smaller than the others (body length: 181.0, 186.0, and 119.5 cm, respectively). PC1 scores were affected by body size, and smaller specimens had smaller PC1 scores. PC2 scores were not affected by body size. All specimens were clearly divided into two morphological groups: A and B. Group A included six specimens from the coastal waters around the Amami Islands, Amakusa-Shimoshima Island, and Mikura Island. Four of these six specimens (NSMT30133, NSMT32733, KCM-01-000159, and KCM-01-000160) had mitochondrial DNA sequences that differed from those of the *truncatus* type (Kakuda

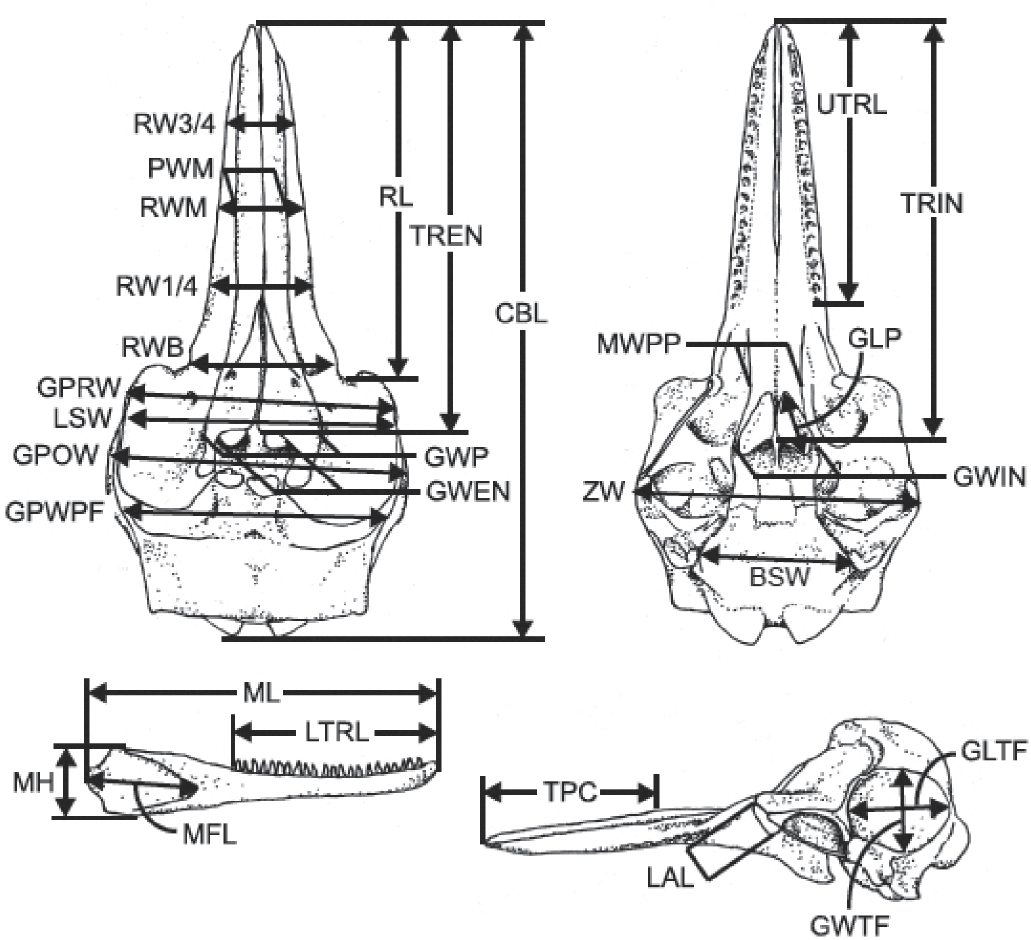

Figure 2. Skull measurements examined (see "Materials and Methods" for character definitions)

Table 1. Principal component weights and eigenvalues from the principal components analysis of characteristics of 25 skulls of bottlenose dolphins

Cranial characters	PC1	PC2
CBL	0.946	0.241
RL	0.710	0.680
RWB	0.880	-0.221
RW1/4	0.911	-0.356
RWM	0.881	-0.418
PWM	0.690	-0.097
RW3/4	0.848	-0.323
TREN	0.862	0.459
TRIN	0.939	0.302
GPRW	0.970	-0.183
GPOW	0.947	-0.243
LSW	0.949	-0.207
GWEN	0.762	0.346
ZW	0.967	-0.175
GWP	0.900	-0.130
GPWPF	0.815	-0.365
GLTF	0.870	0.165
GWTF	0.608	0.171
LAL	0.785	-0.506
GWIN	0.485	-0.068
GLP	0.738	-0.372
UTRL	0.721	0.620
WAS	0.907	-0.252
TPC	0.056	0.762
MWPP	0.788	-0.434
Eigenvalue	4,452.30	768.69
Total variance (%)	76.12	13.14
Cumulative variance (%)	76.12	89.27

et al., 2002; Shirakihara et al., 2003). All other specimens were included in Group B.

Comparison of Groups A and B

Skull characters were compared between Groups A and B using ANCOVA, with CBL as the covariate. Of the 26 characters examined, 17 (RL, RWB, RW1/4, RWM, RW3/4, PWM, TREN, TRIN, GPRW, GPOW, LSW, GWEN, ZW, GWP, GLTF, UTRL, and TPC) were strongly correlated with CBL for both groups ($p < 0.01$), and no difference was detected in the slopes of the regressions between Groups A and B. Therefore, the means of these characters were compared between the groups (Table 2). Nine other characters (GPWPF, GWTF, LAL, GWIN, GLP, BSW, MWPP, NTU, and NTL) were not correlated with CBL ($p > 0.01$); these and CBL were analyzed using Mann-Whitney U-tests (Table 2). Finally, characters that were difficult to measure were compared visually (Figures 4, 5 & 6).

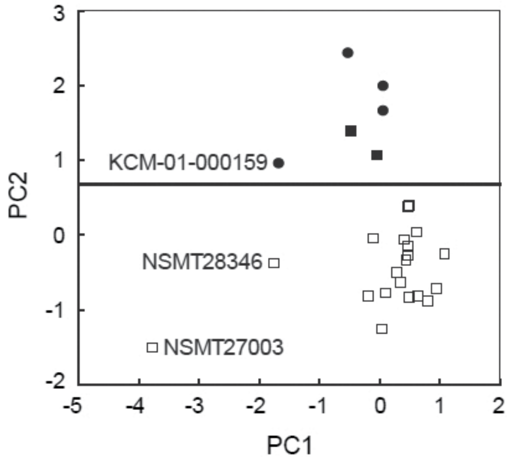

Figure 3. Relationship between the scores of PC1 and PC2 from principal components analysis of skull measurements for 27 bottlenose dolphins from Japanese waters; closed symbols, Group A specimens; open symbols, Group B specimens; closed circles, specimens showing differences from the *truncatus* type in molecular studies (Kakuda et al., 2002; Shirakihara et al., 2003).

For cranium shape, CBL, GPRW, LSW, GWP, and GPWPF were significantly smaller in Group A than in Group B (Table 2); however, the ranges of GPRW, LSW, and GWP overlapped substantially. CBL and GPWPF had no or minimal overlap in their ranges (Figure 7). For tooth count, NTU was larger in Group A than in Group B (Table 2), although the ranges overlapped substantially (A: 25 to 26; B: 21 to 26). In contrast, no significant difference was observed in NTL between the groups, and no significant differences in GLTF and GWTF were found between the groups either (Table 2). In visual comparisons, the width of the parietal in the temporal fossa was much narrower in Group A than in Group B (Figures 4a & 4b).

For the shape of the rostrum, many differences existed between the groups. RW3/4, PWM, TREN, and UTRL differed significantly between the groups (Table 2), although the ranges overlapped substantially. RL, RW1/4, RWM, and TPC were very different between the groups, with no or minimal overlap in ranges (Figure 8); RL and TPC were much larger in Group A than in Group B, whereas RW1/4 and RWM were much smaller in Group A than in Group B. In contrast, no significant difference was detected in RWB between the groups. In visual comparisons, the rostra of Group A tapered abruptly, whereas those of Group B tapered gradually (Figures 5a & 5b). The apex of the premaxillary convexity of Group A was more distinct than that of Group B (Figure 4a & b). In addition, the antero-mediad ridge from the

Table 2. Statistical comparisons of skull measurements between Groups A and B of bottlenose dolphins from Japanese waters

	Group A		Group B		*p*-level	
Characters	*n*	Mean	*n*	Mean	ANCOVA	U-test
CBL	--	477.20	--	53.63	--	0.012*
RL	6	278.33	21	273.54	<0.010**	--
RWB	6	110.63	21	123.02	0.060	--
RW1/4	6	78.33	21	96.44	<0.010**	--
RWM	6	66.31	21	81.92	<0.010**	--
RW3/4	6	49.98	19	60.45	<0.010**	--
PWM	6	37.90	21	44.44	0.021	--
TREN	6	320.49	21	325.59	<0.010**	--
TRIN	6	326.07	20	334.21	0.061	--
GPRW	6	200.92	21	224.60	0.015*	--
GPOW	6	226.41	21	247.58	0.095	--
LSW	6	197.66	21	220.22	0.035*	--
GWEN	6	53.93	21	54.35	0.063	--
ZW	6	226.74	21	248.43	0.076	--
GWP	6	81.11	21	92.64	<0.010**	--
GPWPF	--	174.61	--	206.32	--	<0.010**
GLTF	6	101.83	20	108.14	0.425	--
GWTF	--	73.92	--	75.98	--	0.584
LAL	--	42.89	--	57.83	--	<0.010**
GWIN	--	61.73	--	68.04	--	0.182
GLP	--	61.19	--	73.89	--	0.021*
UTLR	6	232.10	21	231.45	<0.010**	--
WAS	--	112.83	--	125.83	--	0.015*
TPC	6	169.25	21	143.34	<0.010**	--
MWPP	--	36.65	--	53.12	--	<0.001**
NTU	--	25.25	--	23.40	--	0.013*
NTL	--	24.50	--	22.50	--	0.088

Insignificant $*p < 0.05$; $**p < 0.01$

antorbital notch was less prominent in Group A than in Group B (Figures 5a & 5b).

LAL, GLP, BSW, and MWPP were smaller in Group A than in Group B (Table 2), although the ranges of GLP and BSW largely overlapped. Although the mandible-related characters were not compared statistically because of limited data for the Group A specimens, the mandibles of Group A specimens curved upward, whereas those of Group B specimens were straight (Figures 6a & 6b).

Comparison of Japanese Bottlenose Dolphins and Type-Specimen Skulls

To confirm the systematic positions of the two groups of Japanese bottlenose dolphins (*Tursiops* spp.), we compared the skulls of the type specimens of *T. aduncus* and *T. truncatus* with those of *Tursiops* spp. from Japanese waters. The sex of the *T. aduncus*-type specimen was unknown, and its left antorbital process (part of the lachrymal, frontal, and maxilla) was broken. The sex of the *T. truncatus*-type specimen was also unknown, and both mandibles were missing.

The skull of the *T. aduncus*-type specimen was much smaller and more slender than that of the *T. truncatus*-type specimen, indicating that Groups A and B were similar to the type specimens of *T. aduncus* and *T. truncatus*, respectively (Figure 5). In the comparisons of cranium shape between Groups A and B, significant differences were noted, with minimal or no overlap, in the characters CBL, GPWPF, LAL, and MWPP. Therefore, these characters were compared among the two groups and both type skulls (Figure 7). We used raw data because GPWPF, LAL, and MWPP were not correlated with CBL. The CBL of the *T. aduncus*-type specimen was slightly smaller than the range (mean ± SD) of Group A and much smaller than the range of Group B. The CBL of the *T. truncatus*-type specimen was slightly larger than the range of Group B and much larger than the range of Group A. Both the GPWPF and LAL of the *T. aduncus*- and *T. truncatus*-type specimens fell within the range of Groups A and B, respectively. The MWPP of the *T. aduncus*-type specimen fell within the range of Group A, whereas that of the

T. truncatus-type specimen was slightly larger than the range of Group B and much larger than the range of Group A. In visual comparisons, the *T. aduncus*-type specimen had a much narrower parietal within the temporal fossa than the *T. truncatus*-type specimen, suggesting that Groups A and B resembled the *T. aduncus*- and *T. truncatus*-type specimens, respectively (Figure 4).

The *T. aduncus*-type specimen had considerably more teeth on the upper jaw than the *T. truncatus*-type specimen (*T. aduncus*: 26; *T. truncatus*: 23). Thus, the number of teeth in the *T. aduncus*-type specimen fell within the overlapping range of Groups A and B, whereas that of the *T. truncatus*-type specimen fell within the range of Group B.

We compared the rostrum shape among Groups A and B and the *T. aduncus*- and *T. truncatus*-type specimens because many differences in rostrum shape occurred between the two groups from Japanese waters. In particular, RL, RW1/4, and TPC showed minimal overlap between the groups, and those of the *T. aduncus*- and *T. truncatus*-type specimens fell within the ranges of Groups A and B, respectively (Figure 8). In visual comparisons, the rostrum of the *T. aduncus*-type specimen was abruptly narrow about one-quarter of the rostrum length from the base of the rostrum, whereas that of the *T. truncatus*-type specimen tapered gradually (Figures 5c & 5d). The antero-mediad ridge from the antorbital notch was not prominent in the *T. aduncus*-type specimen, whereas that of the *T. truncatus*-type specimen was prominent (Figures 5c & 5d). This indicates that Groups A and B were similar to the type specimens of *T. aduncus* and *T. truncatus*, respectively. In contrast, the apex of the premaxillary convexity was obvious in both type specimen skulls, although the apex of Group A was more obvious than that of Group B (Figure 4).

In the mandible comparison, both the *T. aduncus*-type specimen and Group A specimens had an upwardly curved mandible up at the anterior tip, which differed from that of the Group B specimens (Figure 6). The *T. truncatus*-type specimen was not compared because the mandibles were missing.

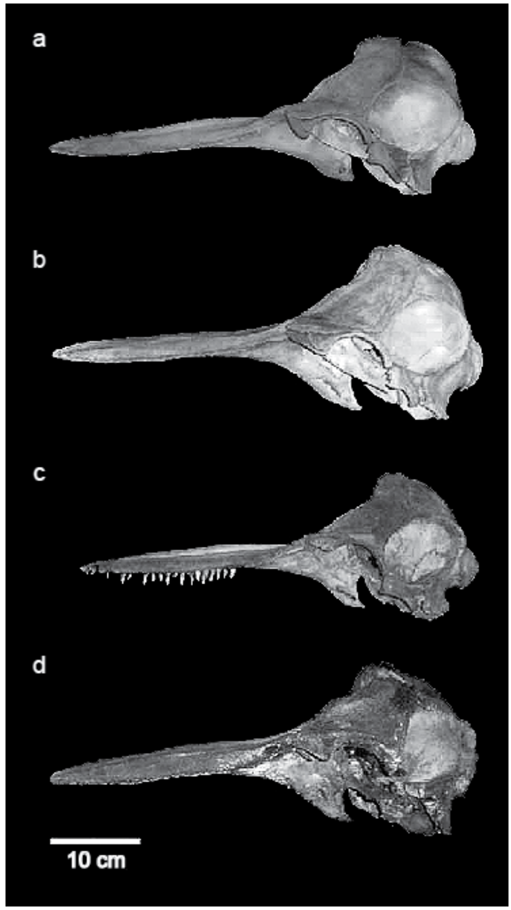

Figure 4. Lateral view of the skull of (a) NSMT30133 (Group A), (b) NSMT21327 (Group B), (c) ZMB6640 (*Tursiops aduncus*-type specimen), and (d) NHM353a (*T. truncatus*-type specimen)

Discussion

The taxonomy of bottlenose dolphins (*Tursiops* spp.) is confusing. Many authors have recently suggested the occurrence of two species, *T. truncatus* and *T. aduncus*, and two or more morphotypes resembling *T. truncatus* and *T. aduncus* (or *T. cf. aduncus*) have been described from many localities (van Bree, 1966; Ross, 1977; Wang et al., 1999, 2000a, 2000b; Hale et al., 2000). LeDuc et al. (1999) showed that *T. aduncus* was distinct from *T. truncatus* using molecular analysis, but found that *T. aduncus* was similar to *Stenella* spp. and not *T. truncatus*. This result reflected that cytochrome b could not be used to establish the true mitochondrial taxonomy. Most systematic conclusions on *Tursiops* are based on the studies of van Bree (1966) and Ross (1977). Van Bree (1966) suggested the occurrence of *T. aduncus* from Mossel Bay, South Africa, and although he did not investigate the type specimens, he described useful characters with which to identify the species. Ross (1977) suggested that *T. aduncus* and *T. truncatus* in South African waters were separate species because of their sympatric distribution and compared them to the type specimens of *T. truncatus*, *T. aduncus*, *T. catalania*, and *T. absulam*. Information from the type specimens of *T. truncatus* and *T. aduncus* is still limited, however. Therefore, to clarify the systematic of the genus *Tursiops*, local studies and the examination of type specimens are necessary.

Figure 5. Dorsal view of the skull of (a) NSMT30133 (Group A), (b) NSMT21327 (Group B), (c) ZMB6640 (*Tursiops aduncus*-type specimen), and (d) NHM353a (*T. truncatus*-type specimen)

We analyzed the skulls of 27 bottlenose dolphins from Japanese waters and compared them to the type specimens of *T. aduncus* and *T. truncatus*, dividing the Japanese bottlenose dolphins into two morphological groups: A and B. Group A comprised six specimens from the coastal waters of Mikura Island, Amakusa-Shimoshima Island, and the Amami Islands, and Group B included 21 specimens from other waters around Japan. Morphological differences between the groups were not related to geographic variation because Group A specimens were similar to the *T. aduncus*-type specimen from Belhosse Island, Red Sea, rather than Group B specimens. Group B specimens were consistent with the *T. truncatus*-type specimen from Dunncanon Pool, Devonshire, UK. These results support molecular studies of Japanese bottlenose dolphins (Kakuda et al., 2002; Shirakihara et al., 2003). Kakuda et al. (2002) showed that two bottlenose dolphins (NSMT30133 and NSMT32733) from Mikura Island waters were clearly distinguishable from *truncatus*-type specimens and were similar to *T. aduncus* from Chinese waters (Wang et al., 1999). Shirakihara et al. (2003) also described the morphology and genetics of two bottlenose dolphins (KCM-01-000159 and KCM-01-000160) from around Amakusa-Shimoshima Island, which resembled *T. aduncus* from Indonesia and South Africa.

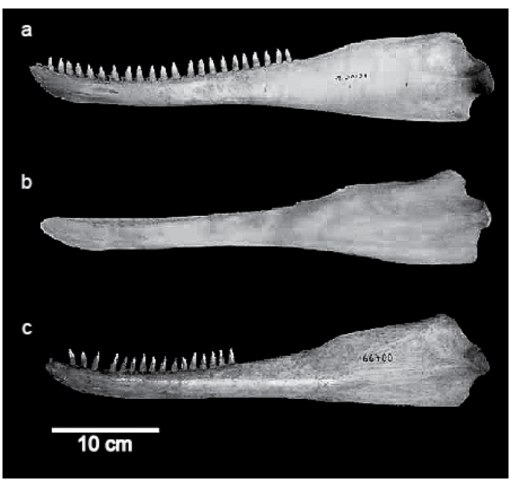

Figure 6. Lateral view of the mandibles of (a) NSMT30133 (Group A), (b) NSMT21327 (Group B), and (c) ZMB6640 (*Tursiops aduncus*-type specimen)

Morphometric characters were used to identify the two groups. The ratios of various skull measurements to CBL have been used to discriminate between the two species in several studies (Ross, 1977; Wang et al., 2000a; Kemper, 2004). Wang et al. (2000a) noted some skull ratios with which to identify *T. aduncus* and *T. truncatus* in Chinese waters; however, we found that many of the skull ratios (TREN, RW3/4, PWM, GPRW, LSW, GWP, GLP, UTRL, and BSW) overlapped substantially, although significant differences were observed between the two groups. These results may be attributable to morphological variation related to body length, although this was not fully investigated. The RL, RW1/4, RWM, and TPC of grown specimens differed greatly between the two morphological groups from Japanese waters. The rostrum of Group A was longer and narrower than that of Group B. According to Ross (1977), Wang et al. (2000a), and Kemper (2004), *T. aduncus* has a

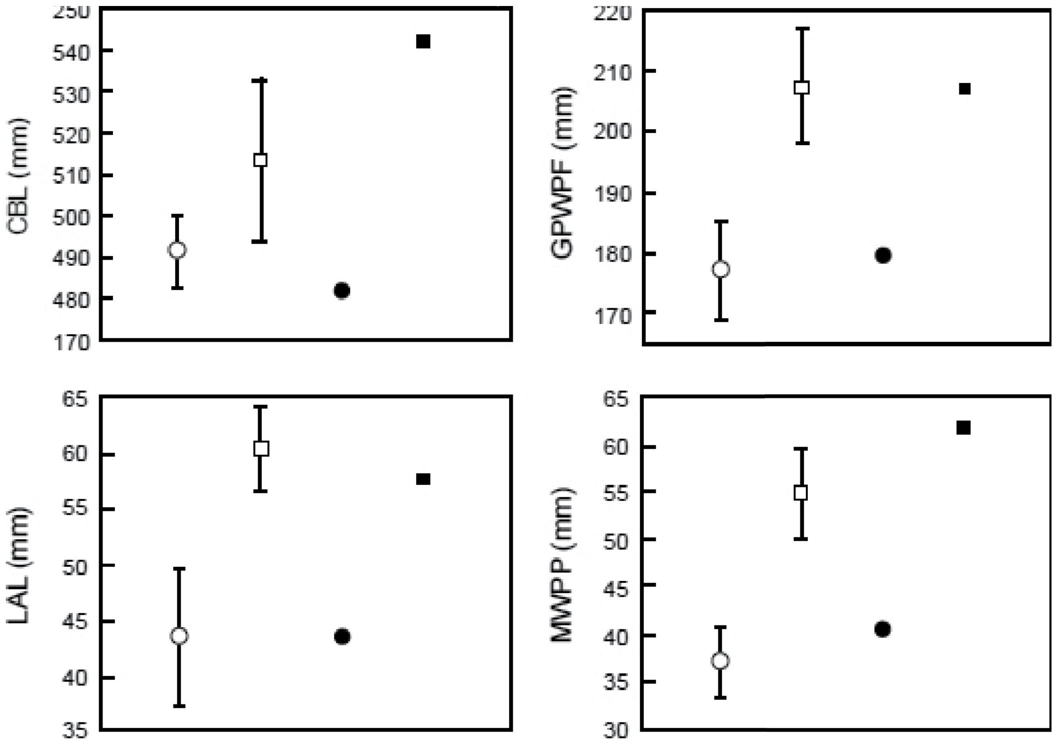

Figure 7. Comparisons of the characters CBL, LAL, GPWPF, and MWPP among Group A, Group B, and the *Tursiops aduncus*- and *T. truncatus*-type specimens (see "Materials and Methods" for character definitions); open circles, mean of Group A; open squares, mean of Group B; closed circles, *T. aduncus*-type specimen; closed squares, *T. truncatus*-type specimen. Bars indicate ranges (mean ± SD) calculated from the measurements of the specimens, excluding the small specimens KCM-01-000159, NSMT28346, and NSMT27003.

longer, narrower rostrum than *T. truncatus* in South African, Chinese, and southern Australian waters. The *T. aduncus*-type specimen also had a long, narrow rostrum compared to the *T. truncatus*-type specimen. Therefore, the differences in these characters may be common between *T. truncatus* and *T. aduncus* worldwide, and Groups A and B had the features of *T. aduncus* and *T. truncatus*, respectively, in terms of rostrum shape. Some other differences were also observed between the two groups from Japanese waters. The antero-mediad ridge from the antorbital notch of specimens in Group A was less prominent than that of fully grown specimens in Group B. Wang et al. (2000a) suggested that the apex of the premaxillary convexity was more obvious in *T. aduncus* than *T. truncatus* from Chinese waters. Similar differences were also observed in Japanese specimens (i.e., the apex of Group A was clearer than that of Group B). The apex was obvious in both types of specimens' skulls; therefore, this difference may only occur in specimens from Japanese and Chinese waters.

The characters not correlated with CBL were also useful in identifying species because the morphological variation in regards to body size was minimal. GPWPF, LAL, and MWPP were smaller in Group A than in Group B, with no overlap of ranges (mean ± SD). LAL and MWPP were not described as characters useful to distinguish *T. truncatus* and *T. aduncus* in other waters (van Bree, 1966; Ross, 1977; Wang et al., 2000a; Kemper, 2004); however, they were the most obvious features with which to distinguish the two groups in Japanese waters, and those of Groups A and B were similar to those of the *T. aduncus*- and *T. truncatus*-type specimens, respectively. The CBL of Group A and the skull of the *T. aduncus*-type specimen were also much smaller than the CBL of Group B and the skull of the *T. truncatus*-type specimen. This is similar to results of specimens from Chinese and southern Australian waters (Wang et al., 2000a; Kemper, 2004). Even so, Wang et al. (2000a) and Kemper (2004) stated that skull size is not a diagnostic feature with which to distinguish *T. aduncus* and *T. truncatus*. In addition, Group A specimens tended to have more teeth than Group B specimens. This character was not useful in identifying the two groups, however, because the ranges largely overlapped for the upper and lower

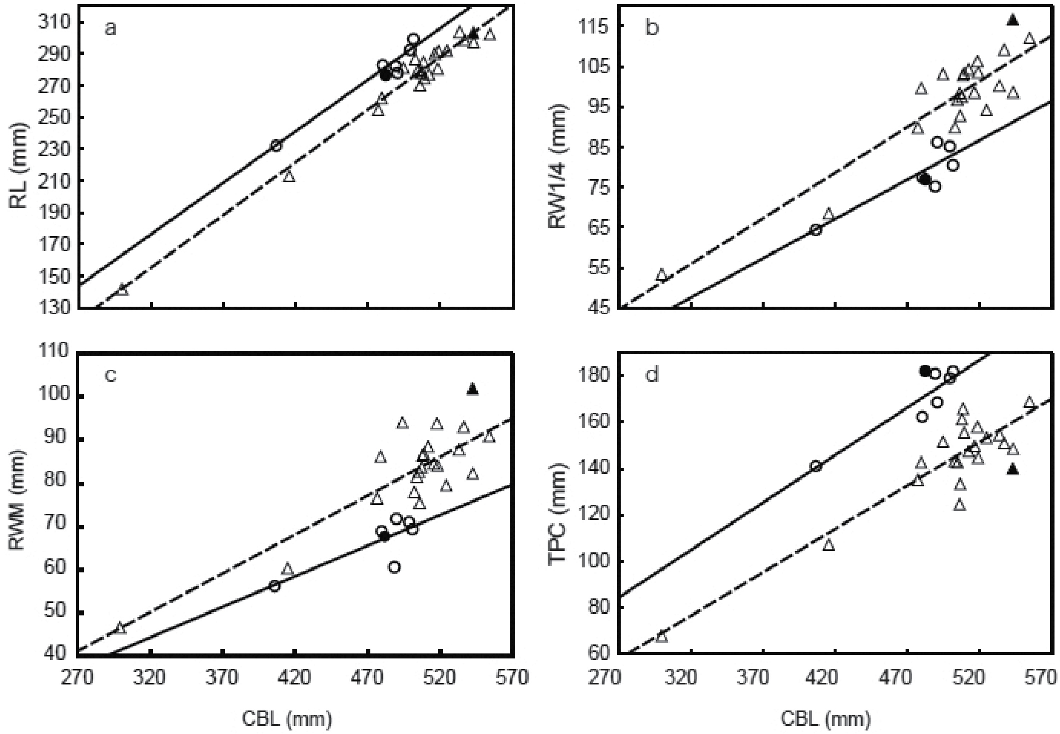

Figure 8. Results of ANCOVA for (a) RL, (b) RW1/4, (c) RWM, and (d) TPC (see "Materials and Methods" for character definitions); open circles, Group A; open triangles, Group B; solid lines, regressions for Group A (a: y = 0.6482x – 30.976; b: y = 0.1957x – 15.076; c: y = 0.1415x – 1.2015; d: y = 0.4097x – 26.266); broken lines, regressions for Group B (a: y = 0.6628x – 56.705; b: y = 0.2273x – 16.816; c: y = 0.1798x – 7.6481; d: y = 0.3747x– 43.341); closed circles, *Tursiops aduncus*-type specimen; closed triangles, *T. truncatus*-type specimen.

jaw in specimens from Japanese waters. No differences occurred in the size of the temporal fossa (GLTF and GWTH) between the two groups from Japanese waters, although Ross & Cockcroft (1990) and Kemper (2004) described the size and shape of the temporal fossa as important in identifying *T. aduncus* and *T. truncatus* from Australian waters.

Numerous opinions have been published on the taxonomy of *Tursiops*. For example, *T. truncatus* and *T. gilli* were also described from around Japan (Ogawa, 1936). Other authors have suggested the occurrence of *truncatus*- and *aduncus*-type bottlenose dolphins from waters around Japan based on patterns of ventral spots (absence and presence, respectively; Miyazaki & Nakayama, 1989; Kasuya et al. 1997; Kakuda et al., 2002; Shirakihara et al., 2003). Although we did not examine external morphology, skull morphology is a distinguishing characteristic useful in discriminating species (Miyazaki, 1994). Two morphological groups (A and B) of bottlenose dolphin from Japanese waters were distinguishable morphologically and were similar to the type specimens of *T. aduncus* and *T. truncatus*, respectively. Therefore, Group A specimens from the waters around the Amami Islands, Amakusa-Shimoshima Island, and Mikura Island were identified as *T. aduncus*, and Group B specimens from other waters around Japan were identified as *T. truncatus*.

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Appendix 1. Core data for the bottlenose dolphin skull specimens studied

Museum no.	Species	Sex	Location
HAES0328	*T. truncatus*	M	Toyohashim Aichi, Japan
KCM-01-000159	*T. aduncus*	M	Amakusa, Kumamoto, Japan
KCM-01-000160	*T. aduncus*	M	Amakusa, Kumamoto, Japan
AIW	*T. aduncus*	M	Amakusa, Kumamoto, Japan
NHM353a	*T. truncatus* (Type of *T. truncatus*)	--	Dunncanon Pool, Devonshire, UK
NSMT24935	*T. aduncus*	--	Amami Islands, Kagoshima, Japan
NSMT26992	*T. truncatus*	F	Taiji, Wakayama, Japan
NSMT26993	*T. truncatus*	M	Kawana, Shizuoka, Japan
NSMT26995	*T. truncatus*	F	Taiji, Wakayama, Japan
NSMT27003	*T. truncatus*	M	Shimoda Aquarium (unknown detailed locality), Japan
NSMT27004	*T. truncatus*	F	Shimoda Aquarium (unknown detailed locality), Japan
NSMT27180	*T. truncatus*	--	Shimoda Aquarium (unknown detailed locality), Japan
NSMT28346	*T. truncatus*	F	Shimoda Aquarium (unknown detailed locality), Japan
NSMT29360	*T. truncatus*	F	Shimoda Aquarium (unknown detailed locality), Japan
NSMT29462	*T. truncatus*	F	Tomito, Shizuoka, Japan
NSMT29669	*T. truncatus*	--	--
NSMT29772	*T. truncatus*	--	Shimoda Aquarium, Japan
NSMT29851	*T. truncatus*	F	Shimoda Aquarium, Japan (Taiji, Wakayama, Japan)
NSMT30133	*T. aduncus*	F	Mikura Island, Tokyo, Japan
NSMT30177	*T. truncatus*	M	Shimoda Aquarium (unknown detailed locality), Japan
NSMT31327	*T. truncatus*	F	Awasjima Marinepark (Tomito, Shizuoka), Japan
NSMTR31375	*T. truncatus*	--	Joetsu, Niigata, Japan
NSMT31377	*T. truncatus*	--	Awashima Marinepark (unknown detailed locality)
NSMT32417	*T. truncatus*	--	Shimoda Aquarium (unknown detailed locality), Japan
NSMT32418	*T. truncatus*	--	Marine World Umino-Nakamichi, Japan (Taiji, Wakayama), Japan
NSMT32534	*T. truncatus*	F	Tomito, Shizuoka, Japan
NSMT32563	*T. truncatus*	M	Shimoda Aquarium (unknown detailed locality), Japan
NSMT32733	*T. aduncus*	M	Mikura Island, Tokyo, Japan
ZMB6640	*T. aduncus* (Type of *T. aduncus*)	--	Belhosse, Red Sea

All specimens, except type specimens, were from Japanese waters. M, male; F, female; HAES, Experimental Station of Highland Animal Production, Nagoya University, Nagoya, Japan; KCM, Kumamoto City Museum, Kumamoto, Japan; MIE, collection of Amakusa Iruka World, Kumamoto, Japan; NHM, Natural History Museum, London; NSMT, National Science Museum, Tokyo, Japan; ZMB, Museum fur Naturkunde, Berlin.

Appendix 2. Measurements of Groups A and B and the *Tursiops truncatus*- and *T. aduncus*-type specimens

Characters	Group A				Group B				*T. truncatus*	*T. aduncus*
	n	Mean	SD	Range	*n*	Mean	SD	Range		
CBL	5	491.46	8.51	479.60-500.80	19	513.07	19.59	476.80-554.10	542.50	481.65
RL (% CBL)	5	58.49	1.17	56.83-59.86	19	55.28	1.15	53.46-57.11	55.96	57.55
RWB (% CBL)	5	23.34	2.19	21.12-26.53	19	24.94	0.96	23.41-26.47	27.07	24.86
RW1/4 (% CBL)	5	16.49	0.87	15.44-17.63	19	19.53	0.99	17.90-20.89	21.53	16.01
RWM (% CBL)	5	13.90	0.89	12.41-14.65	19	16.56	1.07	14.89-19.01	18.76	14.06
PWM (% CBL)	5	8.01	0.72	6.99-9.03	19	8.97	0.78	7.59-10.23	10.01	7.65
RW3/4 (% CBL)	5	10.79	1.10	9.10-11.84	18	12.11	1.02	9.93-14.03	14.72	11.38
TREN (%CBL)	5	67.39	0.39	67.00-68.04	19	65.76	1.58	62.14-69.37	65.47	66.71
TRIN (% CBL)	5	68.40	0.73	67.22-69.05	18	67.56	1.31	65.17-69.63	67.90	72.17
GPRW (% CBL)	5	42.15	1.32	39.91-43.15	19	45.53	1.91	41.97-49.23	45.48	--
GPOW (% CBL)	5	47.31	1.95	44.43-49.66	19	50.10	2.16	46.76-53.88	51.54	48.79
LSW (% CBL)	5	41.50	1.35	39.41-42.66	19	44.60	2.24	40.53-49.09	45.34	--
GWEN (% CBL)	5	11.31	0.42	10.60-11.65	19	10.98	0.48	9.86-11.64	12.48	11.33
ZW (% CBL)	5	47.60	1.98	44.54-49.52	19	50.31	1.99	47.33-53.98	0.00	47.22
GWP (% CBL)	5	16.97	0.97	15.33-17.68	19	18.72	0.92	16.90-20.45	20.21	17.90
GPWPF (% CBL)	5	36.03	1.42	34.23-37.92	19	40.46	2.21	36.10-45.01	38.18	37.30
GLTF (% CBL)	5	21.46	0.32	21.16-21.89	19	21.32	1.51	18.65-24.45	23.22	22.76
GWTF (% CBL)	5	15.52	1.05	14.19-16.81	19	14.93	0.98	12.51-17.01	--	15.58
LAL (% CBL)	5	8.89	1.30	7.11-10.22	18	11.76	0.76	10.65-13.60	10.63	--
GWIN (% CBL)	5	12.76	1.65	9.91-13.88	17	13.69	1.46	11.43-16.07	12.21	10.95
GLP (% CBL)	5	12.64	2.94	7.77-15.18	16	15.05	0.96	13.22-16.43	15.57	12.59
UTRL (% CBL)	5	48.98	1.08	47.48-50.27	19	46.71	1.42	44.55-49.24	49.38	48.02
LTRL (% CBL)	3	48.98	2.10	47.01-51.19	18	46.50	1.77	43.30-49.69	--	49.56
ML (% CBL)	3	84.69	0.83	84.21-85.64	18	85.94	1.42	82.75-88.30	--	86.29
MH (% CBL)	3	17.34	1.43	16.38-18.98	17	18.30	0.78	17.06-19.90	--	17.50
MFL (% CBL)	3	27.69	1.50	26.80-29.43	18	27.54	2.65	17.73-29.78	--	27.58
WAS (% CBL)	5	23.68	2.08	21.27-26.63	18	25.61	0.98	24.23-27.41	27.41	23.45
TPC (% CBL)	5	35.56	1.33	33.90-37.10	19	29.08	1.87	24.68-32.67	25.85	37.87
MWPP (% CBL)	5	7.56	0.69	6.63-8.55	17	10.70	0.80	9.42-12.21	11.41	8.40
NTU	4	25.25	0.50	25.00-26.00	20	23.40	1.27	22.00-26.00	23.00	26.00
NTL	4	24.50	2.38	21.00-26.00	20	22.50	1.40	19.00-25.00	--	27.00

Means were calculated for specimens, with the exception of the small specimens: KCM-01-000159, NSMT28346, and NSMT27003.