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# Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans

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## Abstract

Two morphological forms of the bottlenose dolphin, *Tursiops truncatus*, are recognised in Indo-Pacific waters; a coastal form referred to as *T. cf. aduncus* and an offshore form, *T. truncatus*. The two are distinguished primarily on the basis of ventral spotting, present in adult *T. cf. aduncus* and absent in *T. truncatus*. We compared the morphology of specimens obtained from parts of their range where both forms are found; south-east Africa, the East and South China Seas, and eastern Australia. Across its range, *T. cf. aduncus* has a shorter body and skull length and on average more teeth than *T. truncatus* from the same areas. No difference in body length was noted between sexes in *T. cf. aduncus*, while male *T. truncatus* were larger than females. *T. cf. aduncus* from tropical waters were distinctly smaller than in subtropical/temperate regions. Differences in the pattern of the dorsal cape between forms from eastern Australia enabled their geographic distribution to be investigated. *T. cf. aduncus* was found in estuarine and near-coastal oceanic waters and *T. truncatus* in near-coastal oceanic and offshore waters. Differences in morphology, and likely niche separation in this partially sympatric distribution of the two forms suggests two species, but there are arguments both for and against the assignment of species status to each morphotype.

Key words: bottlenose dolphin, morphology, distribution, habitat.

## Introduction

Several species of the bottlenose dolphins, *Tursiops truncatus* Montague 1821, have been described. They include *inter alia T. aduncus* Ehrenberg 1832, *T. gilli* Dall 1873, *T. gephyreus* Lahille 1908 and *T. nuannu* Andrews 1911. The specific status of these different forms remains unresolved and only one species, *T. truncatus*, is recognised at present by most authors (Ross and Cockroft, 1990; but see Le Duc *et al.,* 1999). *T. cf. aduncus* is distinguished from *T. truncatus* by distinct ventral spotting in adults. It has a shorter adult body length, smaller skull, and on average more teeth and fewer vertebrae than *T. truncatus* from the same geographic region (Ross, 1977, 1984; Gao *et al.*, 1995).

The *T. truncatus* morphotype has been recorded in tropical and temperate regions throughout the world (Ross, 1977, 1984; Zhou & Quian, 1985; Gao *et al*., 1995; Hersch & Duffield 1990; Van Waerebeek *et al*., 1990; Mead & Potter, 1990, 1995). The *T. cf. aduncus* morphotype is known from coastal and shallow offshore areas in tropical and subtropical waters of the Indo-Pacific region. These include the continental coastlines of the Indian Ocean (Pilleri & Gihr, 1973; Ross, 1977; Robineau and Rose, 1984; Ross, 1984; Ross & Cockroft, 1990), Southeast Asian waters north to the East China Sea (Hammond & Leatherwood, 1984; Tas'an & Leatherwood, 1984; Zhou & Quian, 1985; Harwood & Hembree, 1987; Gao *et al*., 1995), New Caledonia (C. Garrique, pers. comm.), and the east coast and tentatively the west coast of Australia (Ross & Cockroft, 1990). There are no records of *T. cf. aduncus* from the eastern Pacific Ocean or the Atlantic Ocean, although a distinct inshore form of *T. truncatus* was described along the Pacific coasts of North and South America (Walker, 1981; Van Waerebeek *et al*., 1990) and the Atlantic coast of North America (Hersh & Duffield, 1990; Mead & Potter, 1990, 1995).

The aim of the study was to examine the morphology of *T. cf. aduncus* from different parts of its range and to compare its morphology to that of *T. truncatus* from three regions where both forms

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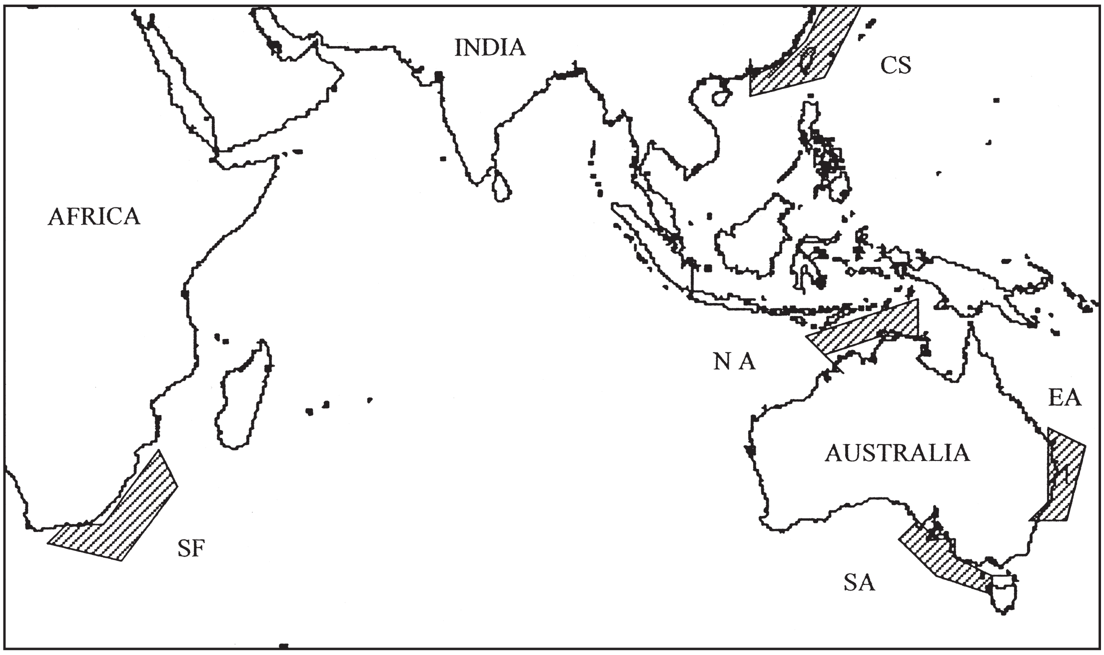


**Figure 1.** Map of the Indo-Pacific region showing localities of specimens analysed in the study; EA: Eastern Australia, NA: Northern Australia, SF: South-east Africa, CS: East and South China Seas, SA: Southern Australia.

are sympatric; the south-east coast of Africa (Ross, 1977, 1984), the East and South China Seas (Gao *et al.*, 1995) and the east coast of Australia (Fig.1). We tested whether there are consistent morphological differences between the two forms throughout the range of *T. cf. aduncus*. We have documented the relative distribution of the two morphotypes in eastern Australian waters to investigate habitat preferences and look for regions of habitat sympatry.

## Materials and Methods

Individual *Tursiops* were classified as adult according to published criteria: significant tooth wear, closure of the tooth pulp cavity, fusion of the vertebral epiphyses to the vertebral centrum, the presence of sperm in the epididymis or testes, at least one *corpus luteum* or *corpus albicans* in the ovary, evidence of lactation and $\geq 10$ dentinal growth layer groups (Ross & Cockroft, 1990; Mead & Potter, 1990; Gao *et al.*, 1995). Individuals held in oceanaria were classed as adult if they had an estimated age greater than 10 years when taken from the wild. Only the individuals classed as adults, by the above criteria, were used to avoid including specimens that were not fully grown or where growth may have been atypical as a result of confinement in oceanaria.

Tooth counts and body and skull length measurements were made using the procedure of Ross (1977). Body length was taken from the tip of the upper jaw to the deepest part of the notch in the flukes. Skull length was the condylobasal length (CBL), measured from the posterior part of the occipital condyles to the anterior point of the rostrum. Tooth counts, for the upper and lower jaws, were all made from skulls and consisted of the number of teeth on the left side, corresponding to the minimum tooth count of Ross (1977) and that of Gao *et al.* (1995).

Carcasses of adult *Tursiops* and live individuals held in oceanaria were identified as *T. cf. aduncus* by the presence of distinct ventral spotting. The colour pattern on the dorsal surface of fresh carcasses and dolphins held in oceanaria were examined, either directly or from photographs, to look for differences in the dorsal cape (cf. Mitchell, 1970; Perrin, 1975; Jefferson *et al.*, 1994). Carcasses were beachcast or recovered from gill-nets (Harwood & Hembree, 1987) or nets set to protect beaches from sharks (Gribble *et al.*, 1998).

Data on body length, skull length, tooth count and spotting in adult *Tursiops* were obtained from

**Table 1.** Sample sizes for body and skull lengths of adult *T. cf. aduncus* and *T. cf. truncatus* from five regions, data for south-eastern Africa are taken from Ross (1977, 1984) and for the East and South China Seas from Gao *et al*. (1995). SL: number of skull lengths, BL: number of body lengths, BL/SL: number of specimens from which both body and skull length were obtained, TC: number of specimens for which a tooth count was available.

| | *T. cf. aduncus* | | | | *T. truncatus* | | | |
|---|---|---|---|---|---|---|---|---|
| Region | BL | SL | (BL/SL) | TC | BL | SL | (BL/SL) | TC |
| Eastern Australia | 21 | 11 | (7) | 6 | 14 | 6 | (5) | 4 |
| Northern Australia | 62 | 15 | — | 1 | — | — | — | — |
| Southern Australia | — | — | — | — | 10 | 17 | (9) | 9 |
| South-eastern Africa | 27 | 31 | (20) | 31 | 5 | 8 | (5) | 9 |
| E/S China Seas | 5 | 7 | (5) | — | 9 | 10 | (9) | — |

five regions (Fig. 1) and are summarised in Table 1. The regions were:

- Eastern Australia: the coast of Australia between latitudes 24°S and 33°S, including beach-cast specimens, incidentally caught dolphins, and dolphins held in the Sea World (south-eastern Queensland) and Coffs Harbour (northern NSW) oceanaria. The Australian and Queensland Museums hold voucher material.
- Northern Australia: the Arafura and Timor Seas to the north of Australia, where specimens were recovered from the Taiwanese gillnet fishery between 1981 and 1986 (see Harwood & Hembree, 1987) or were beach-cast on the northern coast of Australia between longitudes 126°E and 138°E. The Northern Territory Museum holds voucher material.
- South-eastern Africa: the coast of Africa between latitudes 27°S and 34°S. Data are a subset of those published by Ross (1977, 1984) and specimens were included if they had $\geq 10$ dentinal growth layer groups or were classed as adult by the other criteria.
- East and South China Seas, between latitudes 19°N and 35°N. Data are a subset of those published by Gao *et al*. (1995), with clarification provided by Gao (pers. comm.), whereby specimens were included if they had $\geq 10$ growth layer groups.
- Southern Australia: specimens of *Tursiops* from this region were classified as adult by the criteria used for other regions and were then included as *T. truncatus* in the analyses of sexual dimorphism and skull versus body length if their body length was $\geq 270$ cm. This is the lower limit of the length range for *T. truncatus* from other regions of the study and is greater than the largest recorded length for any *T. cf. aduncus* specimen. We regarded this as a reasonable criterion by which to classify the larger *Tursiops* from Southern Australia as *T. truncatus,* as distinct from a small inshore form found in this region that does not display distinct ventral spotting in adults (Ross and Cockroft, 1990). The Victorian and South Australian Museums hold voucher material.

Morphological data were analysed using non-parametric statistical methods, the Mann–Whitney U-test and the Kruskal–Wallis ANOVA.

Boat-based searches for free-ranging *Tursiops* were conducted to investigate the distribution of the two morphotypes. Vessels of 5 to 20 m in length, traveling at speeds of between 15 and 30 kph, with two to four observers were used. The overall region in which searches were conducted was between 24°S and 29.5°S latitudes and up to 15 nautical miles from the coast (Fig. 4). Searches were conducted throughout the year over 4 years, 1995–1998, when the sea-state was $\leq 4$.

The dorsal colour pattern and geographic position of pods of *Tursiops* was recorded and later plotted using the GIS program ARCVIEW (ESRI, 1996). Pods of *Tursiops* for which a colour pattern type could not be determined were not included in the analysis. The geographic distribution of pods of different types was analysed with regard to bathymetry. The significance of differences in proportions of the two forms of *Tursiops* in different areas was tested using a two-tailed Fisher Exact Test. Bathymetric data and information on sea bottom composition were obtained from nautical charts (DGI, 1988).

The majority of searches were conducted in three areas and these are shaded in Figure 4:

- Moreton Bay, an estuary of about 1000 sq. km. where the greatest depth is 20 m.
- The coast and open waters between latitudes 27.4°S and 28.2°S.
- The northern part of the Great Sandy Strait, an estuary, and part of Hervey Bay, an open bay, where the depth does not exceed 40 m.

**Table 2.** Body lengths of male and female *Tursiops* from three groups of specimens: *T. cf. aduncus* from eastern Australia (EA), the East and South China Seas (CS) and south-eastern Africa (SAF); *T. cf. aduncus* from northern Australia (NA); *T. truncatus* from eastern Australia, the East and South China Seas, south-eastern Africa and southern Australia (SA); the *P*-level is calculated for the difference between means in a Mann–Whitney U-test.

| | | Males | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| Morphotype | Location | n | mean | SD | n | mean | SD | *P*-level |
| *T. cf. aduncus* | EA | 11 | 229.5 | 15.00 | 7 | 228.6 | 8.75 | |
| | CS | 4 | 225.4 | 7.28 | 1 | 239.2 | — | 0.888 |
| | SAF | 16 | 238.0 | 9.48 | 10 | 235.2 | 12.53 | |
| | NA | 18 | 202.1 | 10.50 | 22 | 208.3 | 13.23 | 0.117 |
| *T. truncatus* | EA | 5 | 282.6 | 7.09 | 7 | 279.1 | 12.81 | |
| | CS | 4 | 312.5 | 12.92 | 5 | 290.9 | 7.14 | 0.034 |
| | SAF | 4 | 294.3 | 24.93 | 1 | 279.0 | — | |
| | SA | 5 | 300.8 | 24.34 | 2 | 285.5 | 0.71 | |

## Results

### *Sexual dimorphism*

Males (m) and females (f) in three groups were compared to test for sexual dimorphism in body length (Table 2): *T. cf. aduncus* from eastern Australia, the East and South China Seas and southeastern Africa (M=31, F=18); *T. cf. aduncus* from northern Australia (m=18, f=22); *T. truncatus* from eastern Australia, the East and South China Seas, southeast Africa and southern Australia (m=18, f=15). Body lengths of *T. cf. aduncus* did not differ significantly between the sexes for either of the two groups analysed. Body lengths of male *T. truncatus* were significantly greater than females ($P=0.034$, Mann–Whitney U-test, Table 2).

Skull lengths of male and female *T. cf. aduncus* from eastern Australia, the East and South China Seas and southeast Africa did not differ significantly (m=20, f=11, $P=0.393$), while there was insufficient data to test for sexual dimorphism in *T. cf. aduncus* from northern Australia. There was no significant difference in skull length between male and female *T. truncatus* (m=16, f=8, $P=0.101$). However, a larger female sample would increase the power of this test.

### *Comparison of T. cf. aduncus morphology by region*

Body and skull lengths of adult *T. cf. aduncus* were compared from four regions; south-eastern Africa, the East and South China Seas, eastern Australia and northern Australia (Fig. 1). The mean values for each region are plotted in Figure 2. Specimens of *T. cf. aduncus* from northern Australia had significantly shorter body lengths than those from the other regions (*P* Mann–Whitney U-test). They also had smaller skull lengths ($P<0.05$). There were also small, but significant, differences in the body lengths ($P<0.05$) and in the skull lengths ($P<0.05$) of *T. cf. aduncus* from south-east Africa, the East and South China Seas, and eastern Australia (Kruskall-Wallis ANOVA).

### *Comparison of T. cf. aduncus and T. truncatus morphology*

Body and skull lengths of specimens of *T. cf. aduncus,* and *T. truncatus* from south-eastern Africa, eastern Australia, and the East and South China Seas were compared. There was no overlap in body lengths between the two forms and a small overlap in skull lengths (Fig. 2).

Analysis of tooth counts for *T. cf. aduncus* and *T. truncatus* from south-eastern Africa and eastern Australia revealed modal, but significant, differences (Table 3). Analysis of Gao *et al.* (1995), for specimens from the East and South China Seas, showed a similar result (Table 3).

### *Correlation between body and skull length*

Both body and skull lengths were obtained for 32 *T. cf. aduncus* and 28 *T. truncatus* (Table 1 & Fig. 2). Regression coefficients were calculated separately for the two forms and both were significant (*T. cf. aduncus*; $CBL=295.24+0.74214*BL$, n=32, $r=0.471$, $P<0.01$. *T. truncatus*; $CBL=291.92+0.80640*BL$, n=28, $r=0.7059$, $P<0.01$). There was no significant difference between the slope of the regression lines (two-tailed t-test).

### *Morphological type and dorsal colour patterns*

Live *Tursiops* held in oceanaria and fresh carcasses were inspected to determine the presence or absence

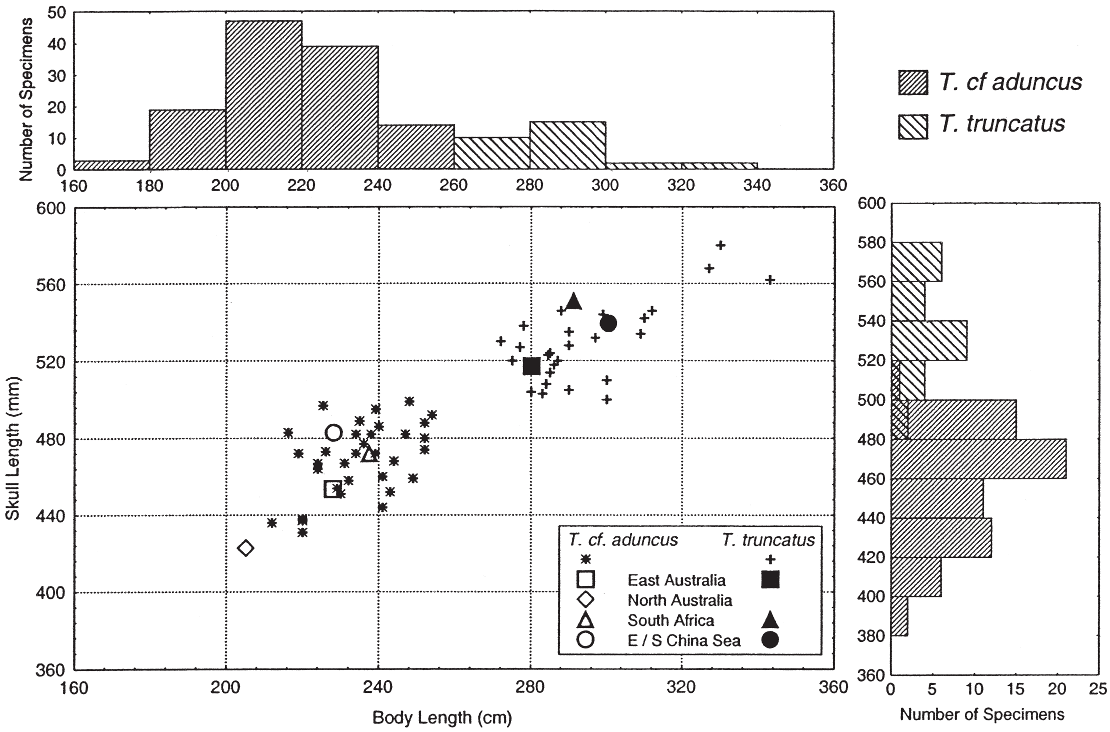


**Figure 2.** Graph and histograms of body and skull lengths of *T. cf. aduncus* and *T. truncatus*. Individual specimens for which both body length and skull length were obtained are plotted as discrete points on the graph. Means for all skull and body lengths, for each region, are also plotted; Eastern Australia, Northern Australia, South-eastern Africa and the East and South China Seas (see Table 1). Histograms show all body (top) and skull (right) lengths obtained for *T. truncatus* and *T. cf. aduncus* from Eastern Australia, Northern Australia, South-east Africa and the East and South China Seas.

**Table 3.** Tooth counts of *T. cf. aduncus* and *T. truncatus* from south-eastern Africa and eastern Australia; n=number of specimens, x=mean number of teeth per row (left side only, see methods), min=minimum number of teeth, max=maximum number of teeth; the *P*-level is calculated for the difference between means in a Mann–Whitney U-Test and the results of Gao *et al.* (1995) are shown for comparison (h.s.=highly significant).

| | *T. cf. aduncus* | | | | *T. truncatus* | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Tooth characteristic | n | x | min | max | n | x | min | max | *P*-level |
| Upper teeth | 37 | 24.9 | 22 | 28 | 13 | 23.8 | 22 | 26 | <0.0058 |
| Lower teeth | 30 | 25.1 | 22 | 27 | 12 | 21.9 | 21 | 24 | <0.0000 |
| Upper teeth (Gao *et al.*, 1995) | 13 | 24.8 | 23 | 26 | 32 | 24.0 | 18 | 24 | h.s. |
| Lower teeth (Gao *et al.*, 1995) | 13 | 24.8 | 22 | 27 | 29 | 23.1 | 21 | 26 | h.s. |

of ventral spotting and the colour patterns on their dorsal surfaces. The colour pattern resembles those of *Tursiops* described from other regions (Perrin, 1975; Leatherwood & Reeves, 1983; Jefferson *et al.*, 1994) in having a darker grey dorsal cape with a light grey dorsal field lateral to it extending onto the flanks, and an off-white ventral area (Fig. 3). Adult specimens that were identified as *T. truncatus* (n=18) or *T. cf. aduncus* (n=25) on the basis of ventral spotting also could be distinguished by the presence or absence of a blaze in the dorsal cape. We found the cape of *T. truncatus* to have a distinct blaze that is not present in *T.cf. aduncus* (Fig. 3). The cape in *T. truncatus* was indented, at the level of the dorsal fin, by a posteriorly pointed blaze extending from the light grey lateral field. The blaze

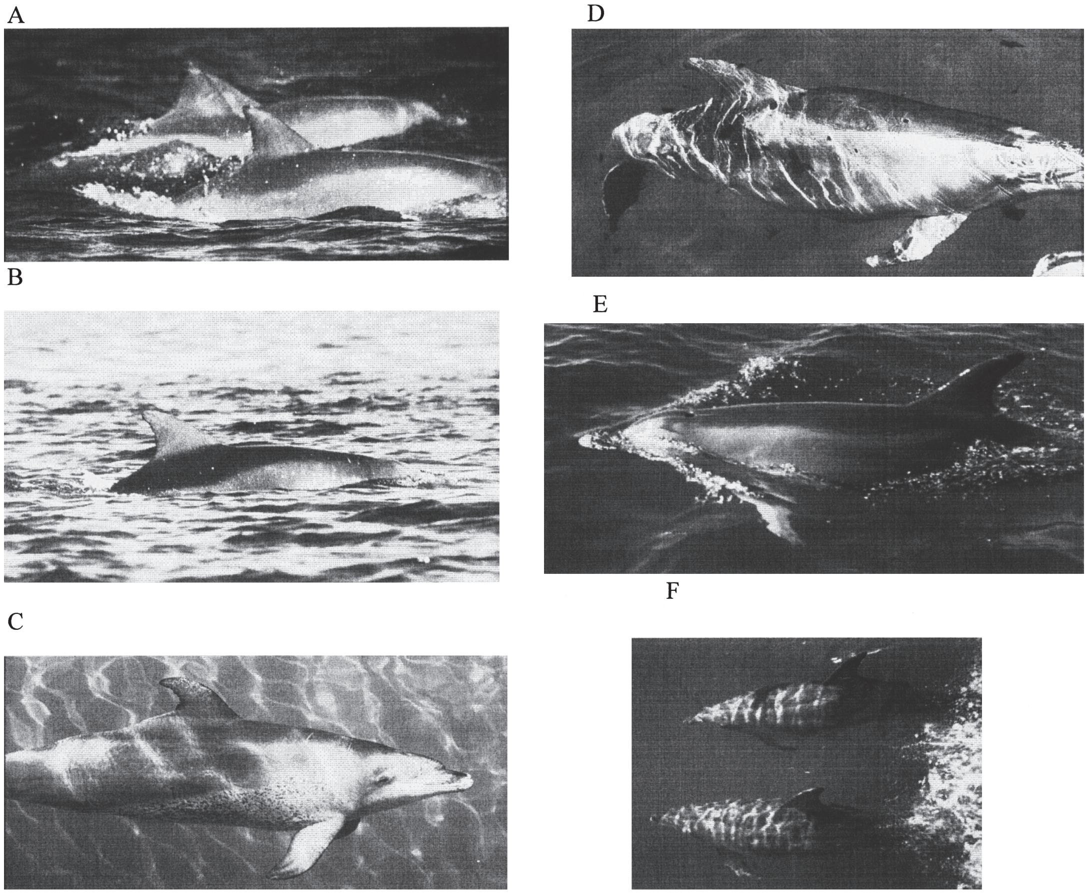


**Figure 3.** Photographs of *T. truncatus* and *T. cf. aduncus* showing the dorsal cape, which in *T. truncatus* has a distinct blaze lateral to the dorsal fin. A: *T. cf. aduncus* off the south-east Queensland coast, B: *T. cf. aduncus* in Moreton Bay, C: *T. cf. aduncus* from the south-eastern Queensland coast at Sea World Oceanarium (note ventral spotting), D: *T. truncatus* from the south-east Queensland coast at Sea World Oceanarium, E and F: *T. truncatus* in Hervey Bay. Refer to Fig. 4 for localities.

also was present in each of four *T. truncatus* calves less than 6 months old, born at the Sea World Oceanarium, Queensland during 1995 and 1996. The dorsal cape and blaze is visible in good light conditions when dolphins surface. Therefore, the presence or absence of a blaze in the cape could be determined reliably in wild, free swimming dolphins.

*Distribution of colour pattern types in the field*

The distinguishing blaze present in the cape of *T. truncatus* from eastern Australia and absent in *T. cf. aduncus* enabled the geographic distribution of the two forms to be studied at sea. On the basis of the blaze, both forms were identified in the study region (Fig. 3). Sightings of pods of *Tursiops* of either colour pattern in Moreton Bay and nearby oceanic waters, as well as the northern part of the Great Sandy Strait and Hervey Bay, are plotted in Figure 4B & C. Only *T. cf. aduncus*, which lacks a blaze, was found in the Moreton Bay and Great Sandy Strait estuaries. Both forms were found in oceanic waters near to Moreton Bay, where a total of 23 surveys were conducted. Pods of *T. cf. aduncus* (A) were sighted more frequently than *T. truncatus* (T) in water <30 m (A=92%, T=8%, n=26), while the opposite was the case in water >30 m, further from the coast (A=26%, T=74%, n=35). The difference in proportions is highly significant (Fisher Exact Test, two-tailed). Searches were conducted in both the warmer and cooler months, so it is likely that the habitat distribution identified is maintained throughout the year. In Hervey Bay, *T. cf. aduncus* was sighted in shallower

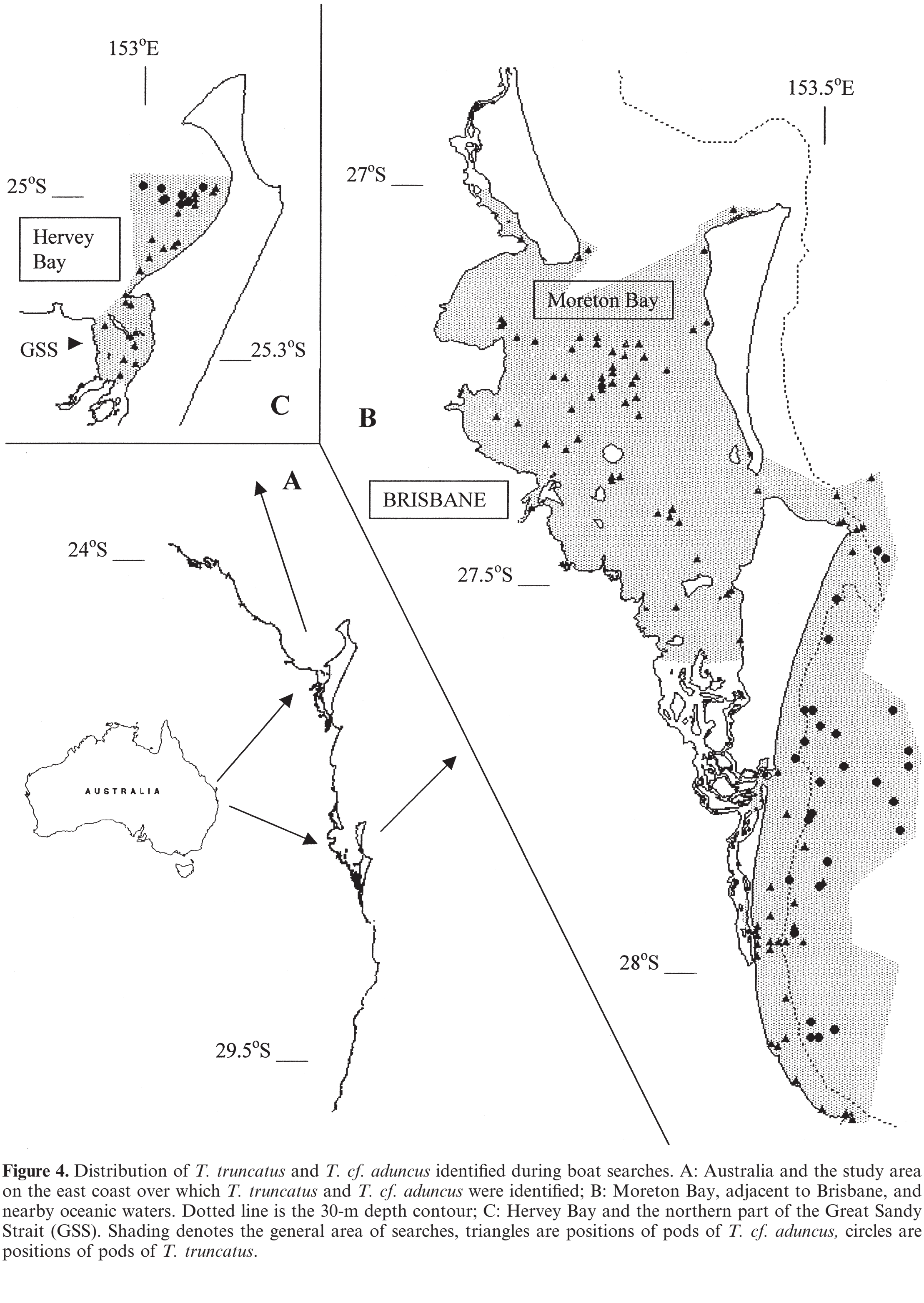


**Figure 4.** Distribution of *T. truncatus* and *T. cf. aduncus* identified during boat searches. A: Australia and the study area on the east coast over which *T. truncatus* and *T. cf. aduncus* were identified; B: Moreton Bay, adjacent to Brisbane, and nearby oceanic waters. Dotted line is the 30-m depth contour; C: Hervey Bay and the northern part of the Great Sandy Strait (GSS). Shading denotes the general area of searches, triangles are positions of pods of *T. cf. aduncus,* circles are positions of pods of *T. truncatus*.

water closer to shore with *T. truncatus* further offshore (Fig. 4C).

## Discussion

The two morphotypes of *Tursiops* identified in this study, *T. truncatus* and *T. cf. aduncus,* showed differences in body length and only a small overlap in skull length. This result was obtained using data from three areas where the two morphotypes have an adjacent or overlapping distribution; south-eastern Africa, the East and South China Seas, and eastern Australia. This finding is evidence that the differences are consistent among the morphotypes and are not due to regional variation. Significant differences in the average number of teeth between the two forms from the three regions also were detected. Mead & Potter (1990, 1995) found modal, but significant, differences in body and skull lengths between *Tursiops* inhabiting coastal versus offshore areas of the western Atlantic Ocean.

We did not find evidence for sexual dimorphism in *T. cf. aduncus,* but did in the body length of *T. truncatus*. Body and skull lengths of inshore *T. truncatus* from the Gulf of Mexico are comparable to those of *T. cf. aduncus,* but they do not exhibit distinct ventral spotting in adults. There is sexual dimorphism in inshore *T. truncatus* from the Gulf of Mexico (Read *et al*., 1993; Tolley *et al*., 1995), suggesting that they may be more akin to *T. truncatus* than to *T. cf. aduncus*.

The finding that *T. cf. aduncus* from south-eastern Africa, the East and South China Seas and eastern Australia are distinctly longer than those from northern Australia could reflect the difference in water temperature between these regions. Sea-surface temperatures in the Timor and Arafura Seas usually are greater than 30°C year round, while those in the other regions, which are subtropical to temperate, do not exceed 25°C (NOAA, 1989). Distinct smaller tropical forms of *Delphinus delphis* (see Pellie, 1985) and *Stenella longirostris* (see Perrin *et al*., 1989) have been documented in Southeast Asian waters. A small form of *S. longirostris,* different from all other forms, has also been described from the Arabian Sea (Van Waerebeek *et al*., 1999).

In southeast Africa, *T. cf. aduncus* is found close to the coast while *T. truncatus* is recorded from deeper water and further offshore (Ross, 1977, 1984). In the East and South China Seas *T. cf. aduncus* is reported at lower latitudes, north to 26°, while *T. truncatus* is reported at higher latitudes (Zhou & Quian, 1985). In the present study, the *T. cf. aduncus* morphotype was recorded in estuaries and shallower oceanic waters close to the coast. The *T. truncatus* morphotype was recorded in both shallow and deeper oceanic waters, but not in the two estuaries, Moreton Bay and the northern part of the Great Sandy Strait. Thus, although there appears to be areas occupied exclusively by each morphotype, there are coastal regions of sympatry in their distributions.

Ross (1977) found that *Tursiops* from southeast African waters feeds predominantly, but not exclusively, on reef dwelling species. The ocean bed over which searches were conducted in the present study comprised approximately equal proportions of sand and rocky reef between the coast and the 200 m depth contour (DGI, 1988). Presumably, *T. truncatus* exploits deeper reefs further offshore, while *T. cf. aduncus* prefers the shallower inshore environment. Ross (1977) also identified differences in the stomach contents of the two morphotypes along the south-east coast of Africa. Mead & Potter (1995) found differences in stomach contents between two morphotypes of *Tursiops* along the eastern seaboard of the United States. In Peru, offshore *Tursiops* consumed mesopelagic fishes and squids not found in coastal *Tursiops.* Inshore demersal fish species found in the stomachs of the coastal form were totally absent in offshore *Tursiops* (Van Waerebeek *et al*., 1990).

The present study revealed both sympatric and distinct distributions of the two morphotypes of *Tursiops*. As the distinct morphology among the forms is maintained despite this sympatry, it is tempting to speculate that they are in fact separate species. However, there are arguments both for and against the assignment of species status to each morphotype:

1. They interbreed freely in captivity and produce fertile female offspring, although it is not known whether male hybrids are fertile. Sterility is a common feature of among species hybrid males (Wu *et al*., 1996).
2. Differences in morphology can be expressions of phenotype, determined by factors such as water temperature and/or depth at which different populations forage. For example, body length differences among *T. cf. aduncus* specimens from tropical *versus* temperate waters and the greater body and skull lengths of *T. truncatus versus T. cf. aduncus* from the same region found in the present study, the differential expression of haemoglobin types in inshore versus offshore bottlenose dolphins from the west coast of America (Hersch and Duffield, 1990), and the decrease in spotting with increasing latitude and cooler water temperature along the south-east coast of Africa (Goodwin *et al*., 1996).
3. DNA sequence analysis of the cytochrome-B gene of mitochondrial DNA (LeDuc *et al*., 1999) reveals that *T. truncatus* and *T. cf. aduncus* are similar genetically to about the same extent as are other species of *Delphininae*. However, conclusions made about species status from analysis

of mitochondrial DNA must be treated with caution. Female natal philopatry, for which there is behavioural (Wells *et al.,* 1987; Scott *et al.,* 1990) and genetic (Dowling & Brown, 1993) evidence in *Tursiops*, can result in a large effective population size for mitochondrial DNA, producing species level sequence divergences among populations (Hoelzer, 1997).

The most compelling evidence for species status in *Tursiops*, although preliminary, comes from recent molecular genetic analysis of nuclear DNA loci (Hale *et al*., in prep.), where genetic material is inherited from both parents. The evidence suggests that in eastern Australian waters the two morphotypes, *T. truncatus* and *T. cf. aduncus*, show a degree of divergence at several nuclear DNA microsatellite loci that is consistent with a molecular taxonomic position as distinct species.

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