MARINE MAMMAL SCIENCE, 18(4):787–818 (October 2002)
© 2002 by the Society for Marine Mammalogy

THE TAXONOMIC STATUS OF THE NOMINAL DOLPHIN SPECIES *DELPHINUS TROPICALIS* VAN BREE, 1971

THOMAS A. JEFFERSON
Hong Kong Cetacean Research Project,
Ocean Park Conservation Foundation,
Ocean Park, Aberdeen, Hong Kong
and
Southwest Fisheries Science Center,
NOAA Fisheries, P. O. Box 271,
La Jolla, California 92038, U.S.A.
E-mail: sclymene@aol.com

KOEN VAN WAEREBEEK
Peruvian Centre for Cetacean Research,
Jorge Chávez, 302,
Pucusana, Peru

ABSTRACT

The taxonomic status of common dolphins in the Atlantic and Pacific oceans has been clarified in recent years, with the discovery that there appear to be two species, a short-beaked (*Delphinus delphis*) and a long-beaked (*D. capensis*) species. However, the taxonomy of common dolphins in the Indian Ocean and southeast Asia is still unclear. A nominal third species, *Delphinus tropicalis* van Bree, 1971, has been described from this area, but its validity is controversial. We reviewed records and literature on common dolphins from South Africa east to Australia and Japan, and measured 206 skulls of common dolphins from the Indo-Pacific and southern California. Other than southern Australia, we found no evidence for *Delphinus delphis* in the Indo-Pacific (South African specimens appear to be *D. capensis*). Previous reports of short-beaked common dolphins in the Indo-Pacific appear to have been cases of misidentification. The *tropicalis*-form has an exceptionally long and narrow rostrum with high tooth counts, but otherwise appears to resemble *D. capensis*, in both skeletal and external morphology. From an examination of 86 *Delphinus* skulls from the reported range of *tropicalis* (Middle East to China), we found that both tooth counts and rostral length/zygomatic width ratios were higher than for 94 *D. capensis* specimens from southern Japan, South Africa, and California. These measurements were greatest in the central Indian Ocean (around India). However, there was evidence of clinal variation, with both decreasing as one moves east or west from India, towards South Africa in the west or Japan in the east. We suggest that the *tropicalis*-form is actually a long-beaked subspecies of *D. capensis*, which may hybridize or intergrade with the standard *capensis*-form in southeast Asia and

possibly along the east coast of Africa. The appropriate name is *Delphinus capensis tropicalis* (van Bree, 1971), and a formal description of the subspecies is provided.

Key words: long-beaked common dolphin, *Delphinus capensis*, *Delphinus tropicalis*, taxonomy, skull morphology, geographic variation, Indo-Pacific region, Indian Ocean.

Despite a great deal of geographical variation, and the existence of at least 30 nominal species (Hershkovitz 1966), until recently common dolphins (genus *Delphinus*) were referred by most cetacean biologists to a single species, *Delphinus delphis* (see Evans 1994). The reason for this was not so much because researchers doubted the existence of multiple species in the genus, but rather that proper studies of geographic variation using adequate series of specimens were largely lacking, and the systematics of the genus was highly confused. Recently, Heyning and Perrin (1994) went a long way towards resolving this confusion with their study of *Delphinus* in the eastern North Pacific. Using a large sample of specimens, most with both external morphometric and skeletal data, they found evidence to support the existence of two species of common dolphins in the eastern North Pacific, short-beaked and long-beaked common dolphins (*Delphinus delphis* and *D. capensis*, respectively). Molecular genetic analysis supported their findings, and showed that short-beaked common dolphins from the eastern North Pacific were more closely related to short-beaked dolphins from the Black Sea than they were to long-beaked dolphins from the same area (Rosel *et al.* 1994).

Although the data set of Heyning and Perrin (1994) was largely restricted to the northeastern Pacific, based on information in the literature they went further to suggest that the two species were also found in other areas of the world. In a global study of geographic variation in the genus, Amaha (1995) also found evidence for discrete long- and short-beaked populations of common dolphins in both the Atlantic and Pacific oceans. However, she was not able to reliably apply the external characters used by Heyning and Perrin (1994) to separate the two species in the eastern Pacific to some other areas. Also, she found evidence for what she interpreted as intermediate forms from Australia and New Zealand (Amaha 1995). She therefore rejected the application of the name *D. capensis* to areas outside the eastern Pacific.[1]

One nominal species, *Delphinus tropicalis* van Bree, 1971, has remained particularly controversial, and Heyning and Perrin (1994) acknowledged that published skull measurements of some specimens from the Indo-Pacific fell well above the range of even the long-beaked species from the eastern Pacific. They, therefore, left open the question of whether *D. tropicalis* was a valid third species in the genus. Rice (1998) in his review of marine mammal species, listed *D. tropicalis* as a separate species, but gave no convincing evidence for doing so.

[1] However, Amaha (1995) failed to take into account the geographical variation that is present within any species. She did not properly consider the possibility that the aberrant forms were simply examples of undocumented geographical variation within the two species recognized by Heyning and Perrin (1994).

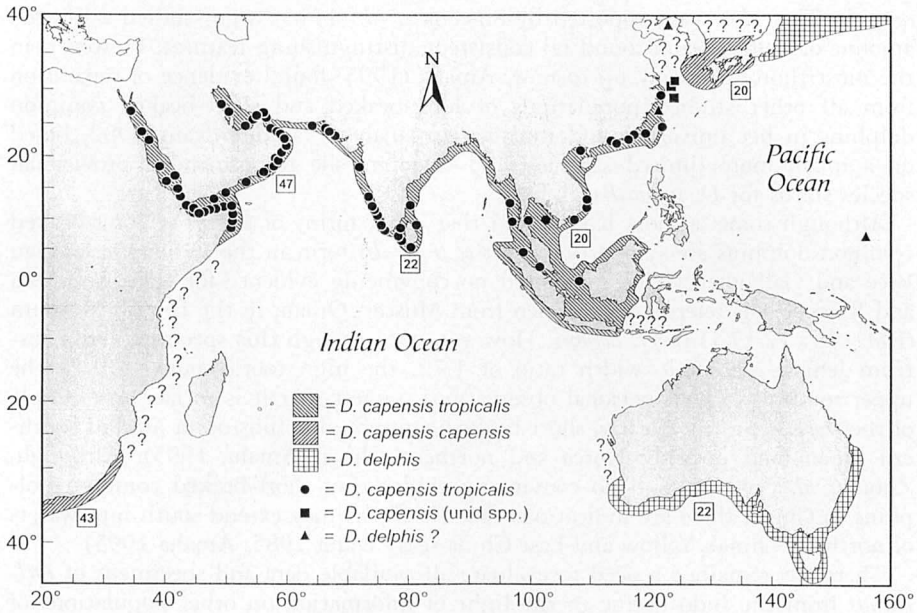


Figure 1. Map of Indo-Pacific region, showing locations of records of *D. capensis tropicalis*, and suspected range of subspecies. There are additional reports of *Delphinus* from Malaysia, Singapore, and Indonesia, but most are considered to be cases of probable mistaken identity (Gibson-Hill 1949, 1950; Lewin 1958; Sigurdsson and Yang 1990). Numbers in boxes show sample size of skulls measured from various geographic regions.

The *tropicalis*-form (as it will be called below) is known from the northeast coast of Africa (Somalia), along the rim of the Indian Ocean, through the western islands of the Indo-Malay archipelago, and northwards to central China (Fig. 1). Its distribution includes semienclosed seas such as the Red Sea, Persian Gulf, and Gulf of Thailand. There are well-known populations of shorter-beaked common dolphins off southern Africa (to about 28°S), southern Japan, and southern Australia (Amaha 1995). However, we were not able to locate any confirmed records of *Delphinus* from elsewhere along the east African coast, nor from northern Australia or the eastern islands of Indonesia/Papua New Guinea (Fig. 1). It is unknown if this is the result of real hiatuses in distribution of the genus, or simply of a lack of research effort in the these poorly studied areas.

Despite a general clarification and increasing stability of cetacean taxonomy in recent years, the taxonomic status of the nominal species *Delphinus tropicalis* has remained controversial. In the early years of modern cetacean taxonomy, it was recognized as valid, and both True (1889) and Flower (1883) maintained it as a separate species. Although it has been listed as a synonym of *Delphinus delphis* in most recent classifications (*e.g.*, Hershkovitz 1966, Rice 1977), some authors have still considered it a valid species (Pilleri and Gihr 1972*a, b*; van Bree and Gallagher 1978; Robineau and Rose 1984; Rice 1998), and others a distinct subspecies (Lal Mohan 1983, 1985*a*; Smeenk *et al.* 1996). Although they did not discount the possibility of species status, Heyning and Perrin (1994) considered that the *tropicalis*-form may represent an extremely long-beaked form of *Delphinus*

capensis. This idea was supported by Smeenk *et al.* (1996), who studied a limited amount of material and found no consistent distinguishing features. However, in the most thorough study up to now, Amaha (1995) found evidence of separation from all other studied populations of long-beaked and short-beaked common dolphins in her univariate and multivariate analyses (as did Evans 1982, based on a much more limited sample), and therefore she recommended provisional species status for *D. tropicalis*.

Although some authors have stated that other forms of short- or long-beaked common dolphins are sympatric with the *tropicalis*-form in the Indian Ocean (van Bree and Gallagher 1978), we found no convincing evidence for this. Robineau and Rose (1984) referred a specimen from Muscat, Oman, in the British Museum (BM 1965.12.17.1) to *D. delphis*. However, even though this specimen has a rostrum length/zygomatic width ratio of 1.72, the high tooth counts (59 in the upper tooth row; TAJ, personal observation) suggest that it is in fact an example of the *tropicalis*-form. Clearly, short-beaked common dolphins occur around southern Japan (and possibly Korea and northern China; Amaha 1995). Although, Zhou *et al.* (1995) found no convincing evidence of short-beaked common dolphins in China, there are indications that *D. delphis* may extend south into waters of northern China's Yellow and East China seas (Wang 1985, Amaha 1995).

There has remained a need to evaluate all available data and specimens of *Delphinus* from the Indo-Pacific in the light of information on other populations of long-beaked common dolphins. Only in this way may the taxonomic status of this form finally become clear. In this paper, we have attempted to do this. We measured as many of the available skulls from the Indo-Pacific as possible, and we analyzed these data along with information on *capensis*-form populations from South Africa, southern Japan, and southern California. We also provide a review of literature on the biology of these animals. In the future, we hope to add information from molecular genetic analyses, currently underway, and to document cranial variation in *Delphinus* samples from the Atlantic and South Pacific oceans.

Methods

We measured a total of 206 skulls of common dolphins, including 153 from the Indo-Pacific (southern Japan to South Africa) encompassing the entire known range of the *tropicalis*-form (Fig. 1, Table 1). In addition, we collected measurements on specimens from southern California ($n = 31$) and Australia ($n = 22$) for comparison (many of the California specimens were also used in the Heyning and Perrin 1994 study). We measured the holotype specimens of *Delphinus longirostris* G. Cuvier, 1829; *Delphinus capensis* Gray, 1828; *Delphinus sao* Gray, 1846; *Delphinus major* Gray, 1866; and *Delphinus pomeegra* Owen, 1866. A list of specimens examined in this study is given in Appendix I, and collection acronyms are presented in Appendix II.

Standard measurements (a subset of those from Perrin 1975, with some minor modifications) were taken on each skull, using vernier calipers and dial calipers (Table 2). Measurements of greater than 10 mm were taken to the nearest millimeter; those of less than 10 mm to the nearest 0.1 millimeter. All measurements were taken by one of the authors (89% by TAJ). Any available data on external appearance and other biological aspects were also gathered. However because most of the specimens were museum acquisitions (many of them very old) and

Table 1. Summary of *Delphinus* skulls measured for this study.

Putative population	Geographic area	No. skulls	Total
South Africa	South Africa	43	43
Middle East	Arabian Peninsula	28	47
	Persian Gulf	7	
	Red Sea	12	
Central Indian Ocean	India	12	22
	Pakistan	10	
Southeast Asia	Vietnam	3	21
	Borneo	1	
	China	14	
	Taiwan	3	
Japan[a]	Japan	19	20
	Korea	1	
Australia[b]	Southern Australia	22	22
California[a]	California, USA	30	31
	Baja California, Mexico	1	
	TOTAL		206

[a] Although short-beaked common dolphins (*D. delphis*) are sympatric in these areas, all of the measured skulls were from long-beaked common dolphins (*D. capensis*).

[b] Identified as short-beaked common dolphins (see text).

not collected as part of a dedicated research program, such information did not exist for the majority of the specimens.

To ensure that there was no significant bias associated with inter-observer differences in how skull measurements were taken, we conducted an intercalibration exercise. Both authors independently measured the same 10 *Delphinus* skulls at two different institutions (the USNM and ZMA), and we compared the means of the resulting measurements using *t*-tests. We used multiple *t*-tests rather than a multivariate MANOVA, because we were interested specifically in identifying which individual measurements showed differences between the way the two authors measured them. This often results from a slightly different spatial interpretation of cranial reference points. We were not interested in examining interactions among the variables here. Only one measurement, length of orbit, exhibited significant differences between the two observers ($P < 0.05$). This measurement was subsequently deleted from further analyses.

For some data analyses, we divided the specimens into seven putative "populations" based on their geographic origin (Table 1). Only cranially adult specimens (defined as specimens with fusion between the maxillae and premaxillae over at least 50% of the length of the dorsal aspect of the rostrum) were used in the analyses of adult dimensions. Perrin and Heyning's (1993) suggestion of using sexual or physical maturity to determine adulthood would not work in this study, due to the large number of specimens without such data. However, the method we used is considered to be a better indication of cranial maturity than distal rostral fusion. The only exception to the criterion of cranial-adulthood was for tooth counts, in which all specimens with accurate tooth counts were included. We followed Amaha (1995), and used the higher count between right and left sides—therefore each specimen was assigned only a single upper and a single lower tooth count.

Table 2. List of measurements and meristics taken on common dolphin skulls.

Character	No. in Perrin (1975)	Abbreviation
Condylobasal length	1	CBL
Length of rostrum	2	LRO
Width of rostrum at base	3	WRB
Width of rostrum at ½ length	5	WRH
Width of rostrum at ¾ length	7	WRT
Width of premaxillae at ½ length	6	WPH
Greatest width of premaxillae	15	GWPM
Preorbital width	10	GPRW
Postorbital width	11	GPOW
Zygomatic width	14	GWZP
Parietal width	16	PARW
Width of external nares	13	GWEN
Width of internal nares	27	GWIN
Length of temporal fossa	19	LTF
Height of temporal fossa	20	HTF
Length of orbit	25	LOR
Length of antorbital process	26	LAPL
Length of upper toothrow	32	LUTR
Depth of palatal groove at ½ length[a]	—	DPG
Length of mandible	38	LMAN
Height of mandible	39	HMAN
Length of mandibular symphysis[a]	—	LMSY
Greatest upper tooth count	33/34	UTC
Greatest lower tooth count	35/36	LTC
Tooth diameter (middle lower left)[a]	—	TD

[a] These measurements were not taken by Perrin (1975).

Although sexual dimorphism is known to occur in some *Delphinus* skull morphometrics (Heyning and Perrin 1994), we did not examine this in the present study. Many of the skulls were museum specimens of unknown gender, and we have no reason to believe that the sample was biased in relation to sex. Therefore, sex was disregarded in this study.

A Principal Components Analysis (PCA) was performed using the software STATISTICA™ V4.1 (Statsoft, Inc.). To be included in analyses of geographical variation, each skull was required to be intact (*i.e.,* the rostrum and brain case could not be missing significant parts), and to be cranially adult. Because multivariate analyses are sensitive to missing data, measurements were excluded if data were missing from more than four specimens. For the remaining measurements with incomplete data, missing values were estimated using the mean substitution method available in STATISTICA™ (this function uses available data from the entire data set to calculate an expected value [mean]). The PCA was performed on the remaining data set ($n = 114$ specimens), which was composed of one meristic (upper tooth count) and 17 morphometric variables.

Results

All specimens examined, except those from southern Australia, were identified as long-beaked common dolphins (*D. capensis* or the nominal *D. tropicalis*), based

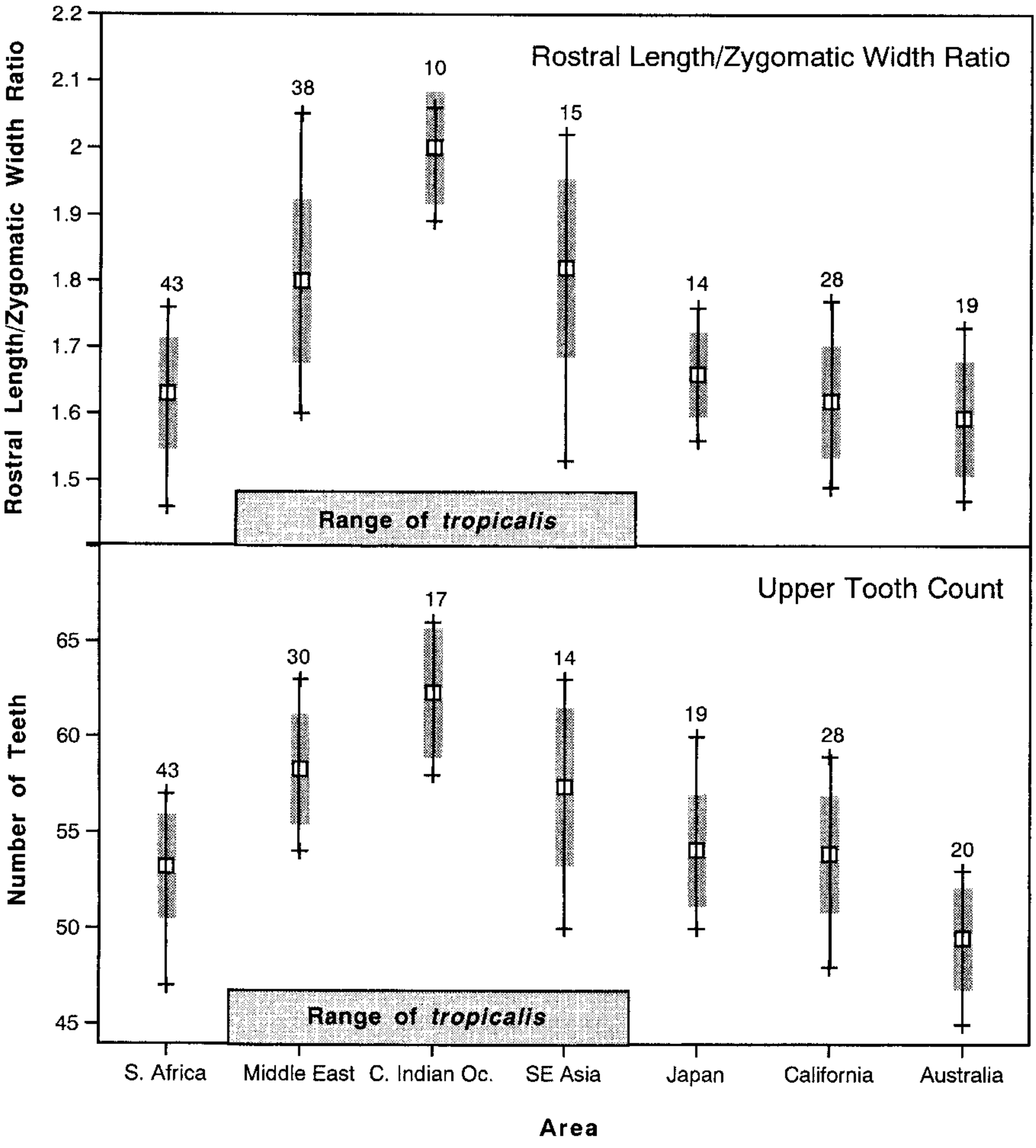


Figure 2. Boxplots of skull dimensions and upper tooth counts by geographic area. Open squares are means, shaded boxes are ±1 standard deviation, vertical bars are ranges, and numbers are sample sizes.

on the features described in Heyning and Perrin (1994). We discovered, as did Amaha (1995), that the Australian specimens did not fit in neatly with the known descriptions of either *D. capensis* or *D. delphis* (they were clearly not associated with the *tropicalis*-form, however). External morphology and color patterns of these animals showed more affinity to *D. delphis*. In terms of cranial morphology, the Australian specimens showed rostral length/zygomatic width ratios only slightly less than those of the long-beaked specimens from the Indo-Pacific and California (indicating their long rostra), but upper tooth counts were much lower (Fig. 2). In fact, tooth count data for these specimens (a range of 45–53 teeth per upper tooth row) fit in quite well with *D. delphis* from southern California (Heyning and Perrin 1994). Their close relationship with *D. delphis* from California has recently been confirmed with molecular genetic data (White 1999). Based on the balance of information, we tentatively assign the southern

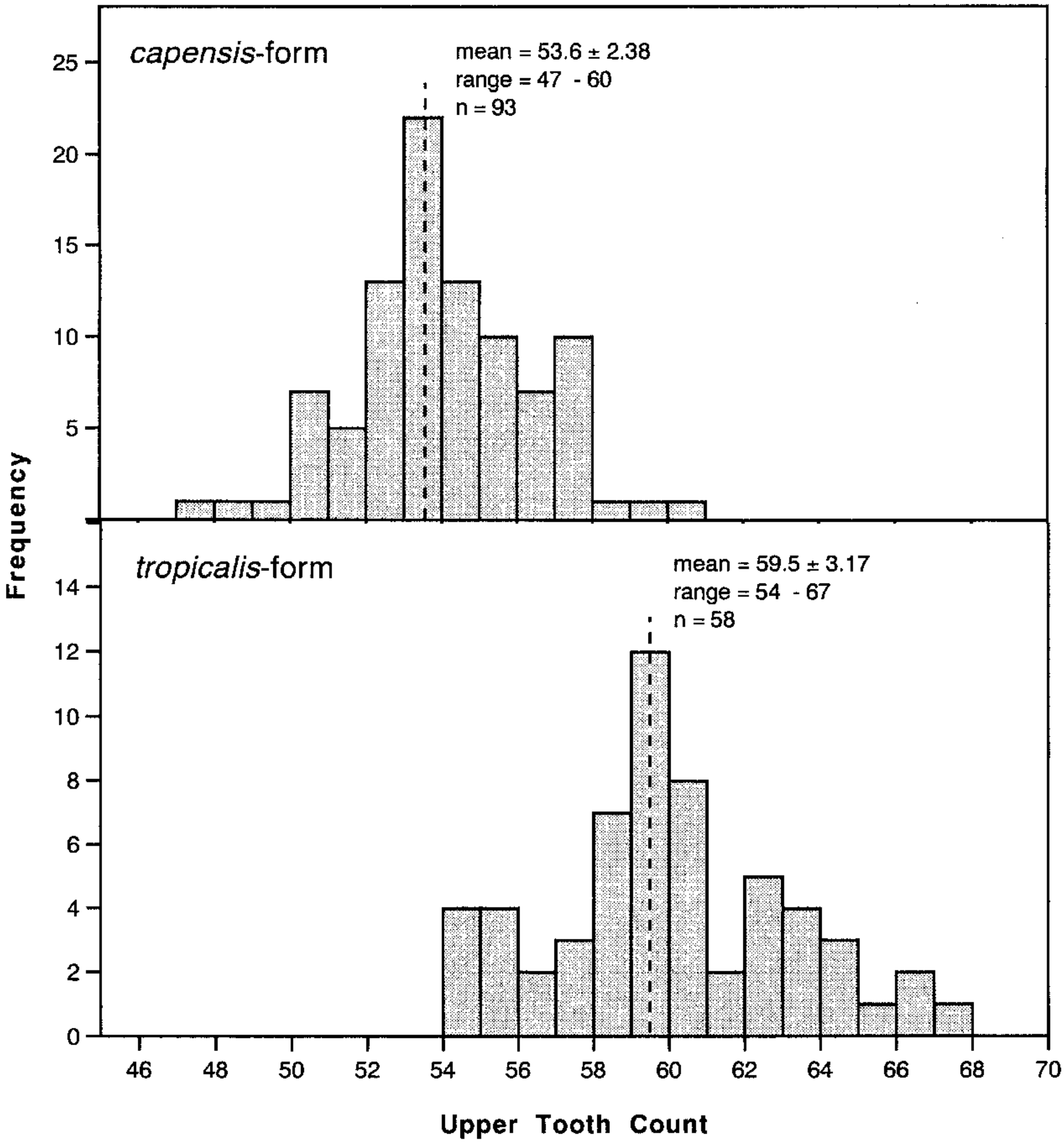


Figure 3. Histogram of upper tooth counts for *capensis*-form and *tropicalis*-form specimens.

Australian specimens to the short-beaked species, *D. delphis*, and do not further consider them in the analyses below.

Among the long-beaked specimens, tooth counts and rostral length/zygomatic width ratios (R/Z ratio) were much higher for *tropicalis*- than for *capensis*-form specimens (Fig. 2, 3, 4). A plot of rostrum length on zygomatic width showed good differentiation of the *tropicalis*- and *capensis*-forms, although there was an area of overlap (Fig. 5). This differentiation was mirrored in the PCA, but the area of overlap was even smaller (Fig. 6). Principal Component 1 explained 40.79% of the overall variation, and PC2 explained 25.20%. The factor loadings for the PCA are shown in Table 3. It is instructive that the type specimen of *D. tropicalis* was at the extreme edge of the *tropicalis* cluster, far from any of the *capensis*-form specimens (Fig. 5, 6).

In plots of R/Z ratio and tooth count data by geographical region, we see that the greatest values for both of these measures are found among the specimens from the central part of the range of *tropicalis* (the central Indian Ocean, Fig. 2).

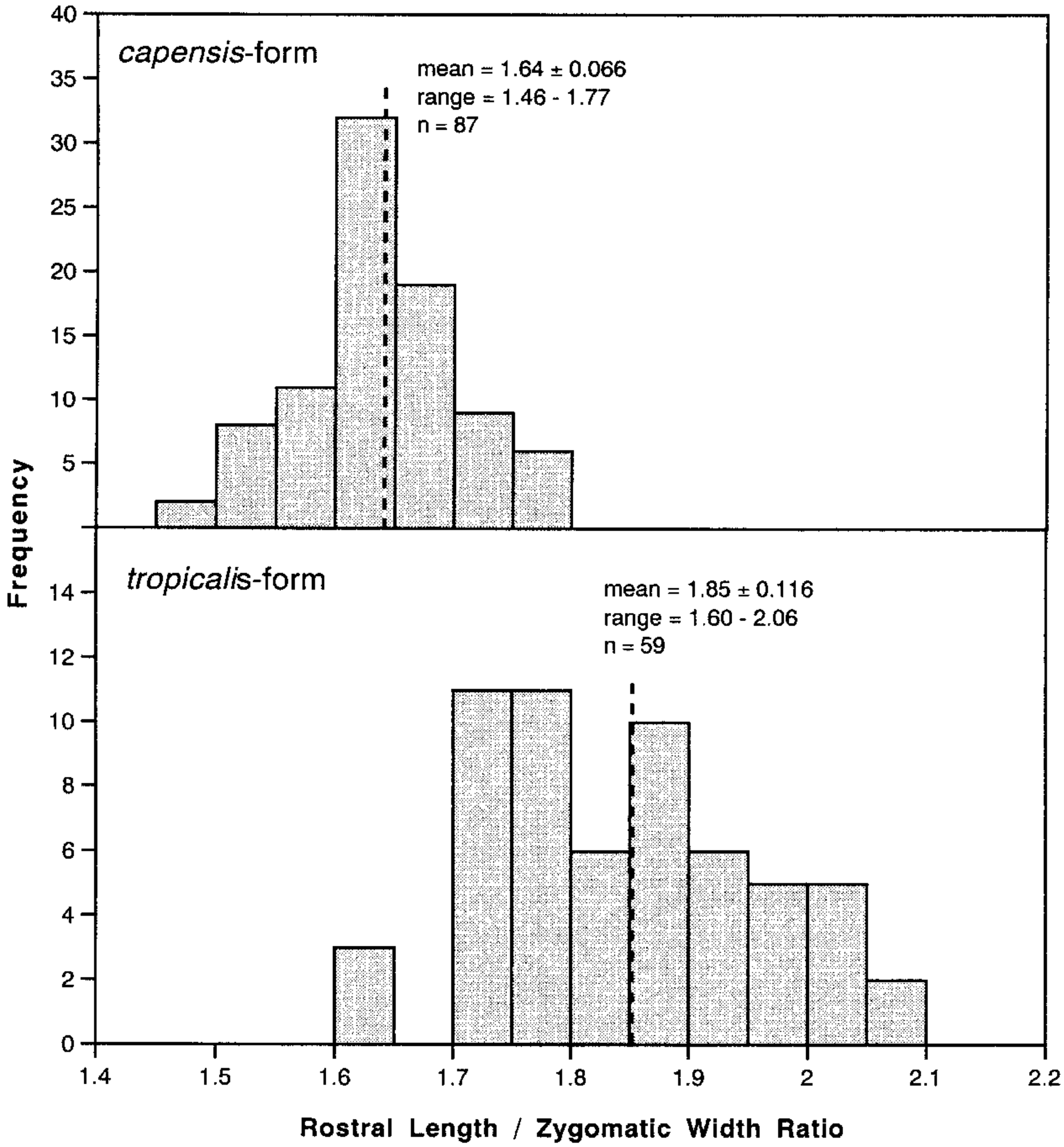


Figure 4. Histogram of rostral length/zygomatic width ratios for *capensis*-form and *tropicalis*-form specimens.

Specimens from both east (southeast Asia) and west (Middle East) of this region show values that are larger than *capensis*-form specimens, but begin to show strong overlap with the South African, Japanese, and southern Californian specimens (all considered standard *capensis*-form).

When we plotted rostral length/zygomatic width ratios and upper tooth counts against collection locality (in degrees longitude), we found further evidence of apparent clinal variation (Fig. 7). The *tropicalis*-form specimens from the central portion of the range (central Indian Ocean) had the highest ratios and tooth counts. Those from the Middle East were lower, and those from southeast Asia were lower yet, showing overlap with those from southern Japan (Fig. 7).

With the two forms well established as unique genetic entities, we examined the data to see which individual cranial characters showed differences. All characters that reflected rostral length or cranial width showed highly sigificant differences between the two forms (Table 4). Overall, 20 characters exhibited significant differences between the two forms, and only six measures did not show differences (Table 4).

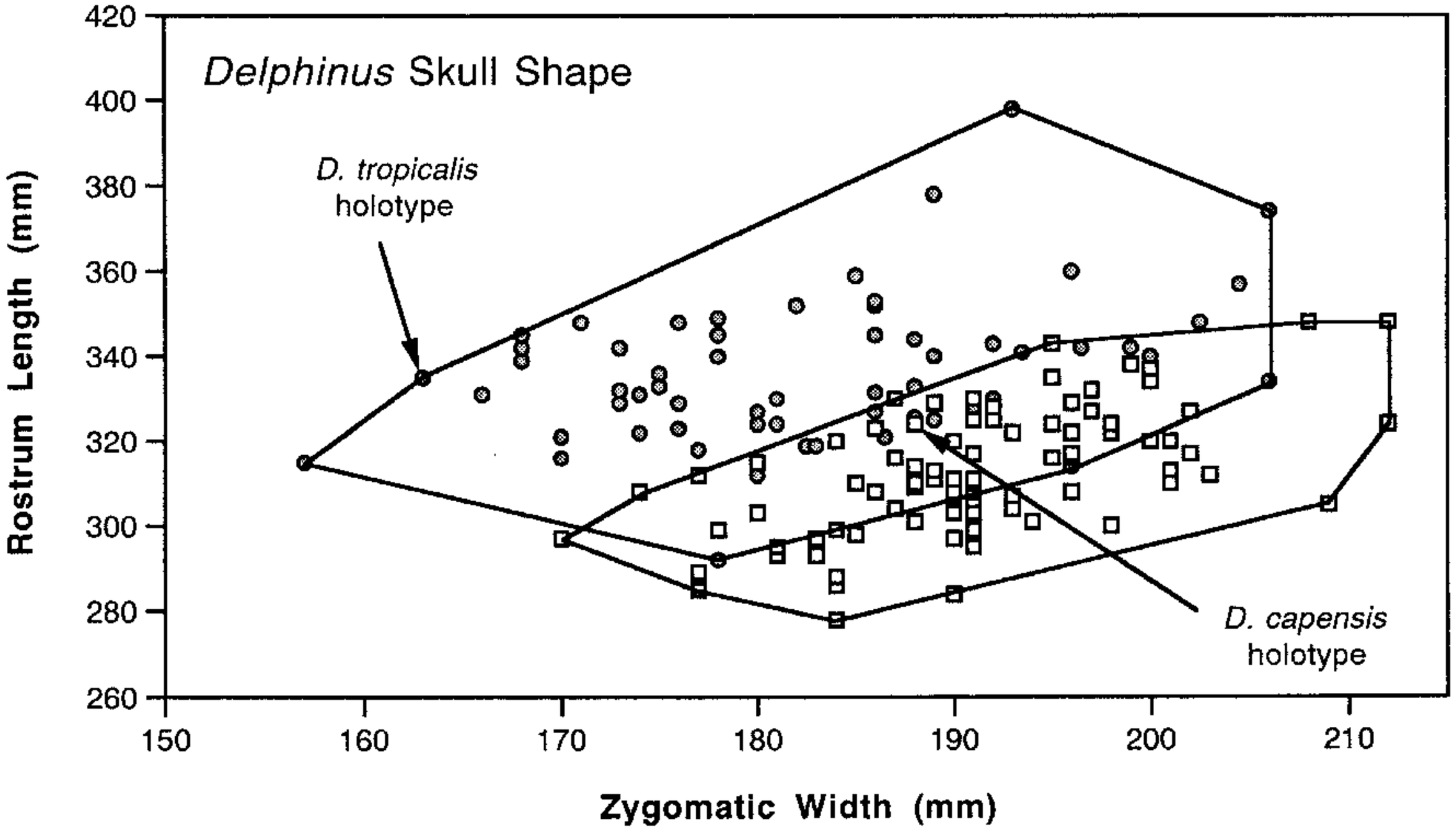
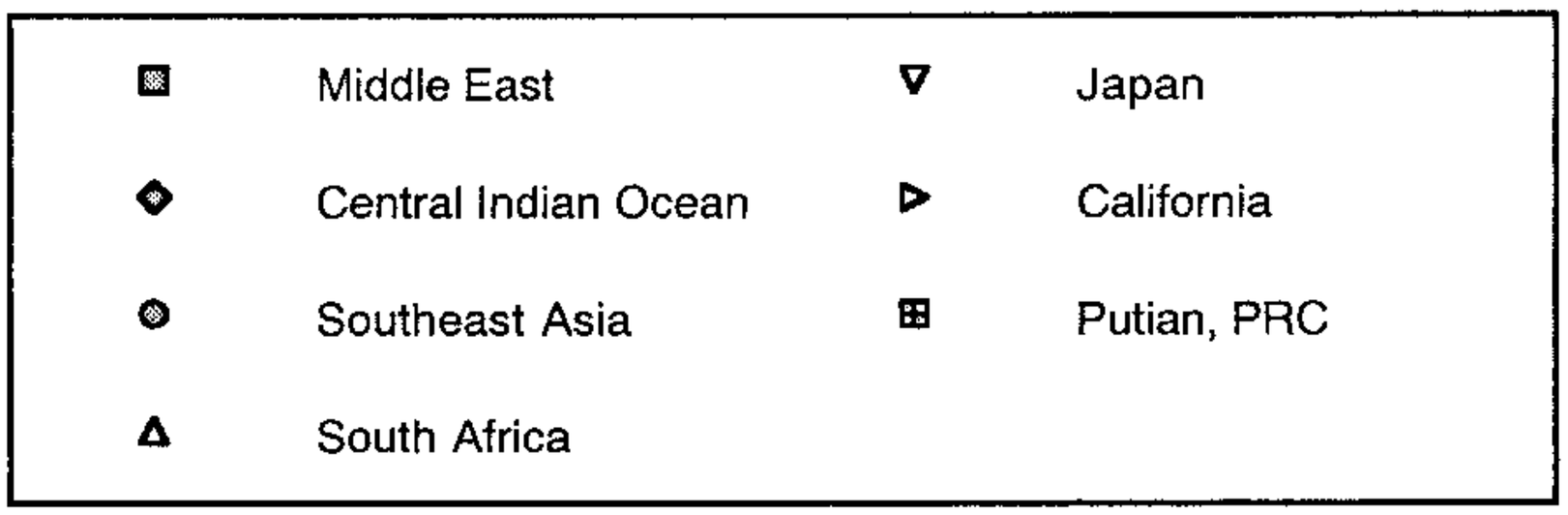


Figure 5. Scatterplot of rostrum length *vs.* zygomatic width for *capensis*-form and *tropicalis*-form specimens.



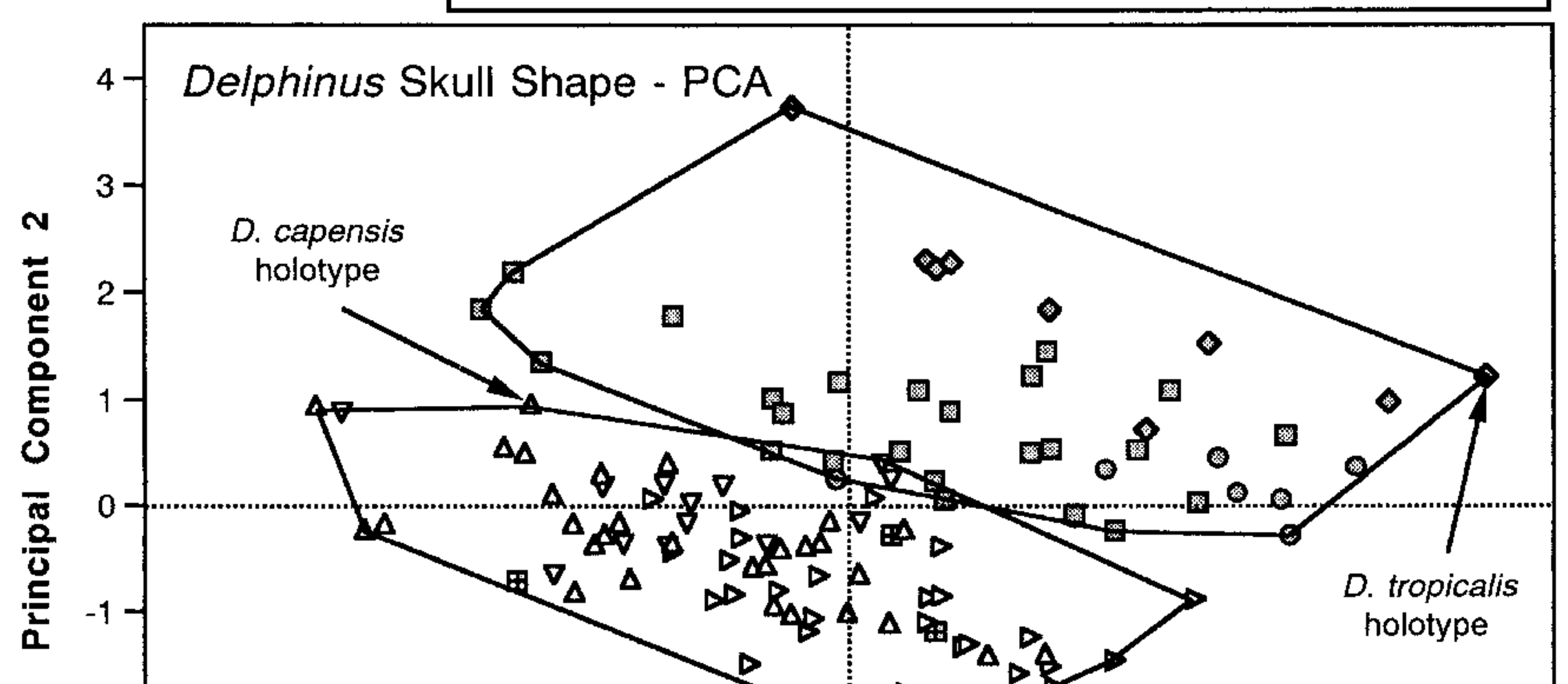


Figure 6. Scatterplot of first two Principal Component scores for *capensis*-form and *tropicalis*-form specimens. Putian specimens are possible intermediates (see footnote 10).

Table 3. Factor loadings for the first two principal components.

Character	Factor 1	Factor 2
Condylobasal length	−0.289	0.910
Length of rostrum	−0.050	0.960
Width of rostrum at base	−0.715	0.393
Width of rostrum at ½ length	−0.819	−0.217
Width of premaxillae at ½ length	−0.676	−0.235
Greatest width of premaxillae	−0.447	0.418
Preorbital width	−0.934	0.026
Postorbital width	−0.949	0.018
Zygomatic width	−0.944	0.048
Parietal width	−0.671	−0.369
Width of external nares	−0.497	0.346
Width of internal nares	−0.832	−0.220
Length of temporal fossa	−0.622	0.309
Height of temporal fossa	−0.318	0.463
Length of antorbital process	−0.691	−0.096
Length of upper toothrow	0.025	0.953
Greatest upper tooth count	0.430	0.721
Rostrum length/zygomatic width ratio	0.599	0.754
Variance	0.408	0.252

Discussion

Taxonomic Status of the tropicalis*-form of Common Dolphin*

It is difficult to fully understand the taxonomic status of a particular form with information from only part of its range. This is certainly true in the present case. There is essentially no information on common dolphins from some very large areas potentially inhabited by the *tropicalis*-form. These include much of the Indo-Malay archipelago, the Bay of Bengal, and the east African coast north of South Africa (see Fig. 1). However, we have obtained data from most major regions of the range of the form, and we feel that our data set is, therefore, representative of the variation exhibited by this form.

The species affiliation of the South African coastal population has remained somewhat controversial in recent years, with most South African authors continuing to refer these specimens to *D. delphis* (Findlay *et al.* 1992, Peddemors 1999). In terms of coloration, South African specimens do not show a clear affinity with either species, as described by Heyning and Perrin (1994). As shown in Figures 2 and 7, the South African cranial data indicated that these animals are long-beaked, and the data fall neatly in line with the *capensis* data from Japan and southern California. We therefore assign these specimens to *D. capensis*. However, there are occasional strandings of specimens in the western Cape area of South Africa that show some differences,[2] and thus it is possible that short-beaked common dolphins (*D. delphis*) may also occur off the South African coast.

[2] Personal communication from P. B. Best, South African Museum, P. O. Box 61, Capetown 8000, South Africa, May 2001.

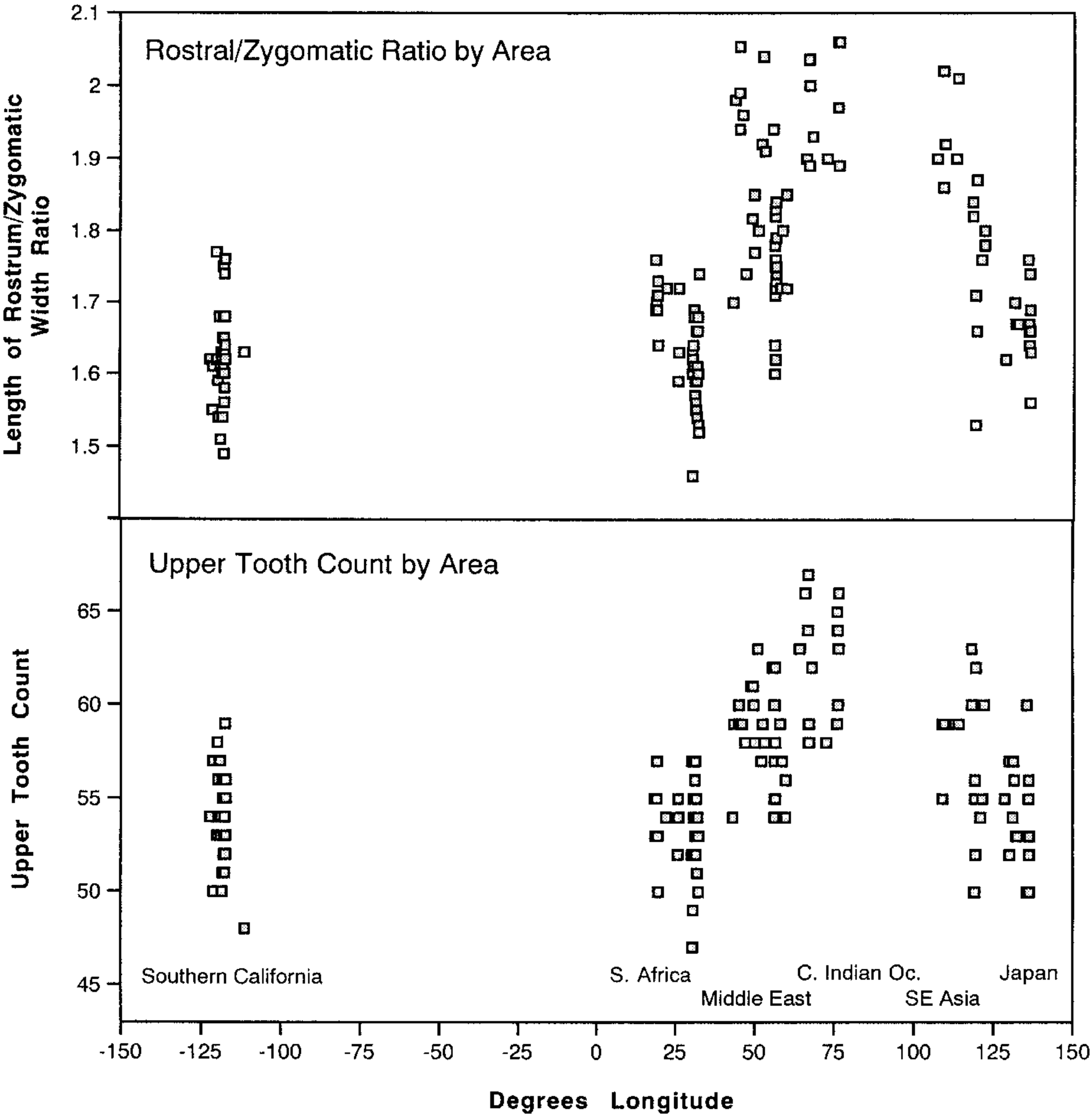


Figure 7. Scatterplot of skull dimensions and upper tooth counts plotted against locality of specimen in degrees longitude.

The pattern that emerges from the available information is as follows: as one moves westward from Japan through southeast Asia, one finds long-beaked common dolphins with increasingly longer rostra and higher tooth counts. This trend reaches its apex in the central Indian Ocean, where there is in fact little or no overlap with specimens from outside the Indo-Pacific. Lal Mohan (1983) also suggested this, although based on a very small sample. As one continues moving west through the Middle East and south to southern Africa, one finds a corresponding decrease in the values for these features. Therefore, although one could perhaps make a preliminary argument for the distinctness of Indian long-beaked common dolphins, when the variation present in the entire Indo-Pacific is brought into the picture, we find evidence of clinal variation at both ends.

As suggested by earlier studies, the *tropicalis*-form common dolphin from the Indian Ocean appears to be a more-or-less distinct form of *Delphinus*, with a narrow skull, extremely long rostrum, and extremely high tooth counts. However,

Table 4. Cranial morphometrics and meristics of adult *Delphinus* specimens.

Measurement	*tropicalis*-form				*capensis*-form				*t*-test;[a] P
	Mean	± SD	Range	*n*	Mean	± SD	Range	*n*	
Upper tooth count	59.5	3.17	54–67	58	53.6	2.38	47–60	93	<0.001
Lower tooth count	57.0	2.93	52–64	44	51.6	2.33	48–57	85	<0.001
Tooth diameter	3.8	0.54	2.8–5.1	36	3.9	0.47	2.9–4.8	39	0.396
Condylobasal length	502.9	21.02	456–575	58	486.0	18.17	449–543	86	<0.001
Length of rostrum	336.2	17.17	298–398	59	312.4	14.51	278–348	87	<0.001
Width of rostrum at base	91.0	7.24	78–112	66	91.2	4.68	80–105	77	0.871
Width of rostrum at ½ length	46.9	4.46	37–58	57	51.8	3.31	45–59	72	<0.001
Width of rostrum at ¾ length	34.4	3.43	27–42	42	39.4	3.16	33–45	72	<0.001
Width of premax, at ½ length	21.0	2.48	16–29	58	22.8	1.87	18–26	71	<0.001
Greatest width of premax.	72.3	4.33	63–86	66	72.2	3.13	64–82	72	0.892
Preorbital width	161.9	9.33	143–185	64	171.1	7.44	154–190	72	<0.001
Postorbital width	184.1	10.31	160–206	63	193.6	8.02	175–217	72	<0.001
Zygomatic width	179.8	11.25	160–206	66	191.1	7.98	170–212	87	<0.001
Parietal width	149.2	7.39	134–166	66	161.4	5.93	148–176	71	<0.001
Width of external nares	46.0	2.87	41–53	66	46.8	2.41	40–52	72	0.074
Width of internal nares	51.3	3.82	42–60	58	57.7	3.17	51–67	70	<0.001
Length of temporal fossa	71.6	5.45	59–85	66	72.8	5.59	61–88	72	0.203
Height of temporal fossa	56.8	4.69	46–66	66	55.7	5.05	40–68	72	0.182
Length of orbit	51.9	2.54	47–59	65	53.9	3.13	46–60	72	<0.001
Length of antorbital process	40.1	4.37	32–52	66	43.6	3.74	37–55	72	<0.001
Length of upper tooth row	291.9	16.62	252–350	59	268.8	12.94	238–304	72	<0.001
Depth of palatal groove	2.8	0.88	1.6–4.7	34	3.4	0.84	1.1–5.6	70	<0.001
Length of mandible	440.8	14.35	419–478	40	420.9	17.64	382–469	75	<0.001
Height of mandible	67.6	4.00	61–77	48	70.6	3.06	64–81	72	<0.001
Length of mandibular symphysis	75.5	9.07	57–95	28	59.3	6.86	44–70	69	<0.001
Rostral length/zygomatic width	1.845	0.1156	1.60–2.06	59	1.637	0.0665	1.46–1.77	87	<0.001

[a] The two forms were established to be different based on the univariate and multivariate statistical tests reported above. Here, we are only testing to see which individual characters differ between the two forms.

two important points must be borne in mind when attempting an assessment of its taxonomic status:

(1) The differences between common dolphins of the *tropicalis* and standard *capensis* forms are largely ones of degree and not of kind. Some overlap exists in essentially all characters examined, and we could find few consistent differences by which to reliably distinguish *tropicalis*. Even these melt away as one moves east or west of the central Indian Ocean.

(2) Where the range of the two putative forms overlap (at least in southeast Asia), the available evidence suggests that interbreeding and, therefore, hybridization or intergradation between the two forms probably occurs.

Therefore, based on the above information, we do not believe that the *tropicalis*-form deserves species status, but instead suggest that it should be recognized as a subspecies of *D. capensis*. A review of nominal species potentially related to this subspecies is presented in Appendix III. The appropriate trinomial is *Delphinus capensis tropicalis* (van Bree, 1971). We provide a formal description of the subspecies below, and also provide a redescription of the standard long-beaked common dolphin (*D. capensis capensis* Gray, 1828), since the *D. capensis* redescription in Heyning and Perrin (1994) is no longer valid.

Redescription of Delphinus capensis tropicalis *(van Bree. 1971)*

Delphinus longirostris G. Cuvier, 1829—Type locality Malabar coast of India (MNHN A-3065, skull only).

Delphinus dussumieri Blanford, 1888[3]—Renaming of *D. longirostris* G. Cuvier.

Delphinus tropicalis van Bree, 1971—Renaming of *D. dussumieri* Blanford.

Holotype and type locality—The holotype consists of a skull stored in the Muséum national d'Histoire naturelle (Paris Museum) with the number MNHN A-3065. The type specimen was collected off the Malabar coast of India by J. J. Dussumier in 1827 (van Bree 1971*b*). The original type description is rather brief; good descriptions and figures of the type specimen were provided by True (1889) and Robineau (1990).

Diagnosis—The color pattern of *D. capensis tropicalis* is generally similar to that of *D. capensis capensis* (Fig. 8, 9; Heyning and Perrin 1994). Smeenk *et al.* (1996) found that the color pattern of animals in the southern Red Sea was "fuzzy" and indistinct, similar to that of *D. capensis*. However, Ballance and Pitman (1998) stated that *tropicalis*-form specimens observed off Oman had a color pattern like that of *D. delphis*, but a body shape like that of *D. capensis* observed in the eastern Pacific. We expect that this is an example of geographic variation in the color pattern.

The only known difference in external morphology between the two subspecies is the longer beak of *D. c. tropicalis*. The length of the beak in this subspecies is about 9.4%–9.7% of the total length (Robineau and Fiquet 1996). We evaluated body length based on the lengths of 70 specimens reported in the literature (Pilleri and Gihr 1972*a*, Yang 1976, Zhou *et al.* 1980, Robineau and Rose 1984, Lal Mohan 1985*b*, James *et al.* 1987, Wang 1990, Salm 1992, Robineau and Fiquet 1996) and 22 unpublished lengths from museum specimens measured by the senior

[3] Generally, a later edition (1891) of Blanford is cited as the reference for the renaming of *D. longirostris* G. Cuvier. However, the correct citation is the earlier edition (Blanford 1888).

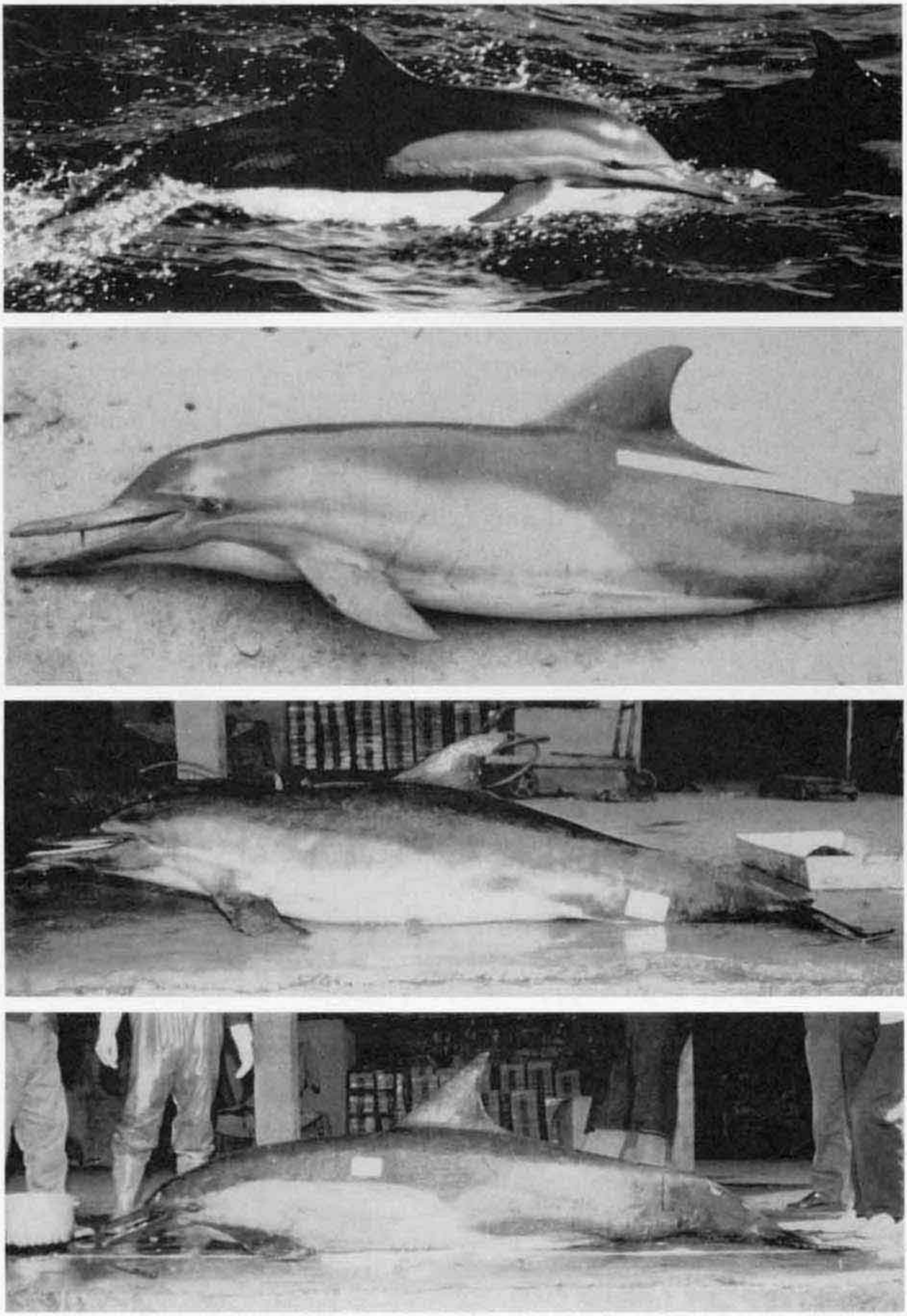


Figure 8. External appearance of *D. capensis* subspecies: *D. c. tropicalis* from off Oman (top) and Nha Trang, Vietnam (upper middle), and *D. capensis* ssp. from Putian, central China (lower middle and bottom). Lower two specimens did not fit well into either *tropicalis* or *capensis* pattern, and may represent intermediates. Photos by R. L. Pitman, Dao Tan Ho, and C. J. Yao.

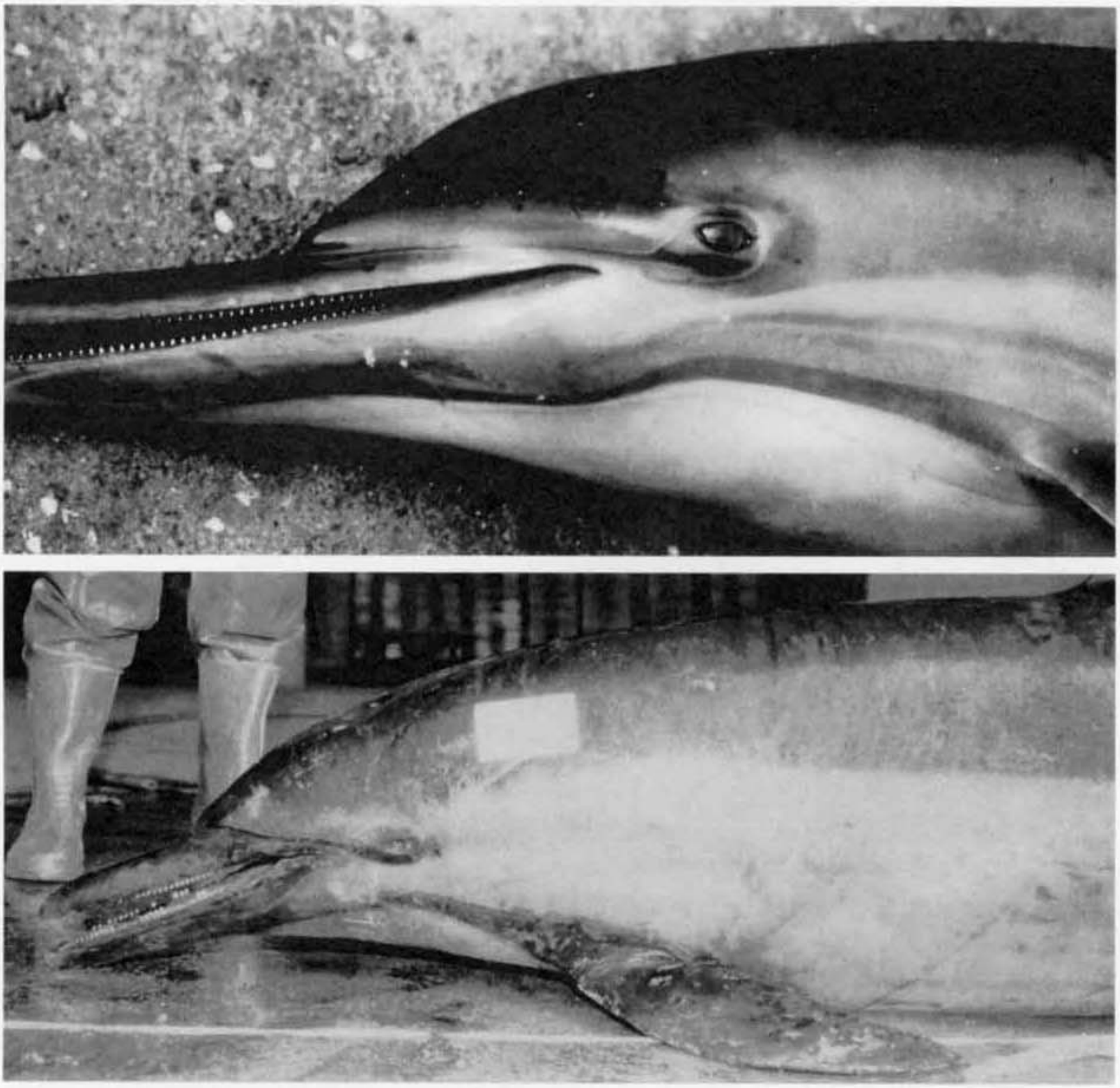


Figure 9. Close up of head of specimen of *D. c. tropicalis* from Nha Trang, Vietnam (top), and unidentified *D. capensis* specimen from Putian, central China (bottom). Photos by Dao Tan Ho and C. J. Yao.

author (TAJ, unpublished data). The total lengths ranged from 100 to 256 cm.[4] From this it can be inferred that this subspecies reaches lengths of at least 260 cm, similar to the *capensis* subspecies. Good photos of the external appearance of these animals can be found in Pilleri and Gihr (1972*a*), Baldwin and Salm (1994), Smith *et al.* (1995, 1997), Zhou *et al.* (1995), and Ballance and Pitman (1998).

Delphinus capensis tropicalis can be distinguished from other long-beaked common dolphins by its narrow skull, extremely long rostrum, and high tooth counts (Fig. 10). The rostral length/zygomatic width ratio of skulls of adult specimens is 1.60–2.06. Upper tooth counts range from 54 to 67 and lower tooth counts from 52 to 64 (although Lal Mohan 1983 reported tooth counts as high as 69). Condylobasal length is, on average, longer than in *D. capensis capensis*, ranging from 456 to 575 mm. Also, the mandibular symphysis is, on average, longer, ranging from

[4] James *et al.* (1987) reported two specimens in the length category 250–299 cm, but the exact lengths were not given.

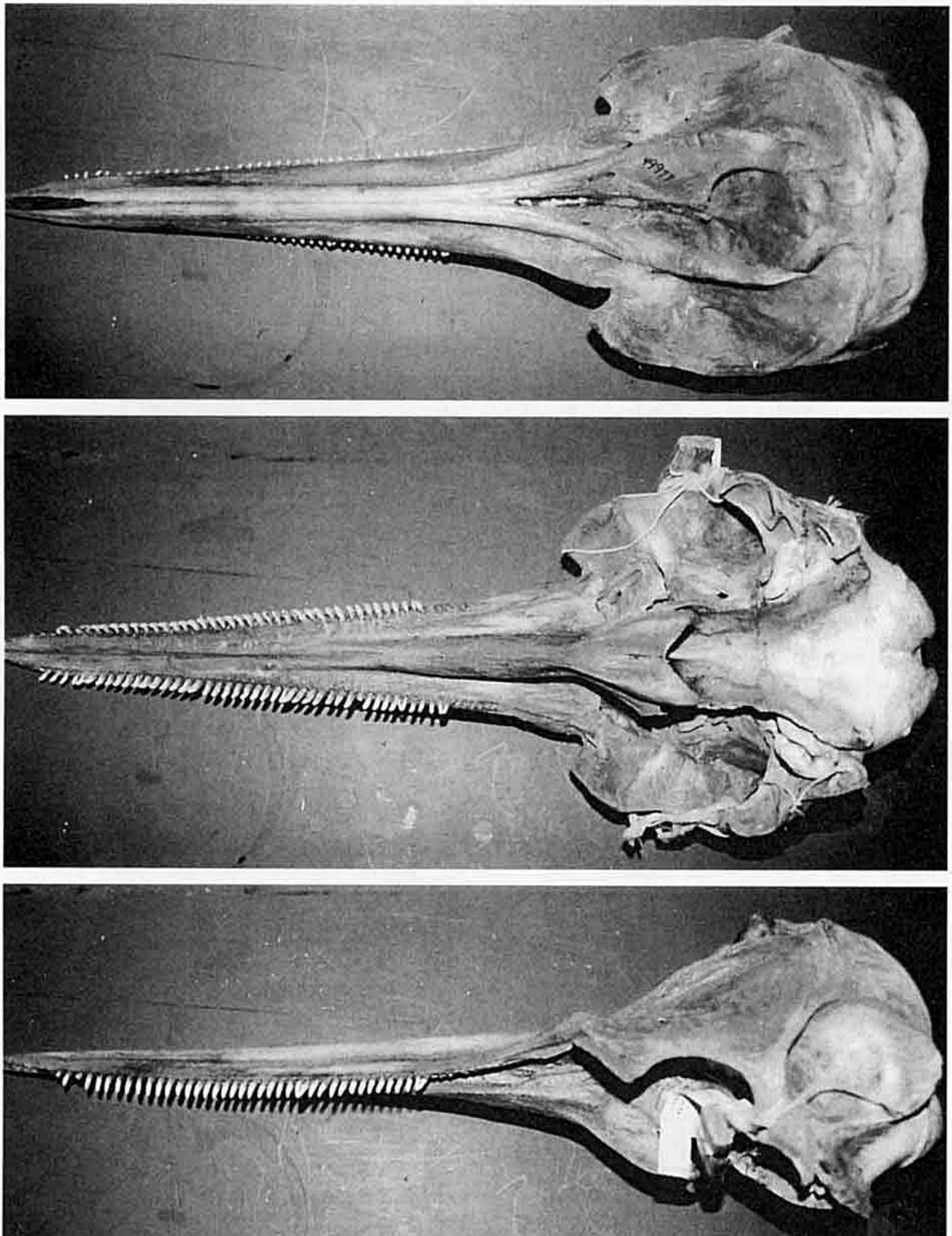


Figure 10. Dorsal (top), ventral (middle), and lateral (bottom) views of skull of specimen of *D. c. tropicalis* from unknown location off west coast of Borneo (USNM 49977; CBL = 493 mm).

57 to 95 mm. Although very few specimens have been examined, Pilleri and Gihr (1972*a*) reported a vertebral formula of C7, T13, L20, Ca31, for a total of 71 vertebrae. The thoracic vertebral count of 13 is lower than in *D. capensis capensis* (Heyning and Perrin 1994), but it remains to be confirmed whether this is a real difference. There are generally 14 pairs of ribs (Pilleri and Gihr 1972*a*).

Geographic variation—There has not been much documentation of geographic variation within the subspecies, but Ballance and Pitman (1998) suggested that specimens off Oman lacked the color pattern characteristics typical of eastern North Pacific *D. capensis* and which also appear to be characteristic of *D. c. tropicalis* in other areas of the Indo-Pacific (*i.e.,* the wide anus stripe and dark facial patterning—see Fig. 8; Baldwin and Salm 1994: p. 35). It is likely that there is, in fact, extensive variation in the color pattern. Both tooth counts and rostral length/zygomatic width ratios appear to be on average much higher for specimens of the central Indian Ocean (collected from India and Pakistan) than for specimens of the Middle East or southeast Asia.

Distribution and habitat—Common dolphins with extremely long beaks have been confirmed to occur from throughout the coastal waters of the Indo-Pacific, from Somalia and the Red Sea in the west, around the rim of the Indian Ocean to western Indonesia and southern China in the east (Fig. 1). There are records of unidentified *Delphinus* from the Yellow and Bohai seas as well (Wang 1979, Shi and Wang 1983), but information in the literature does not allow one to evaluate whether they represent *D. capensis* or *D. delphis*. Likewise, V. G. Cockcroft[5] has observed unidentified *Delphinus* in Kenya and Mozambique. Most of the early specimens of the *tropicalis*-form were collected from the Arabian Peninsula/Persian Gulf area, and until the 1970s the distribution was thought to be limited to the Arabian Sea (Pilleri and Gihr 1972*a, b*). The distribution has recently been extended much farther to the east, to at least Borneo (van Bree and Gallagher 1978), Vietnam (Smith *et al.* 1995), and China (Zhou *et al.* 1980, Parsons *et al.* 1995, Zhou *et al.* 1995). There are apparently only two valid records for the Gulf of Thailand (Chantrapornsyl *et al.* 1996).[6,7] The absence of records from Bangladesh and Burma (Myanmar) can probably be attributed to a lack of marine mammal research effort in marine waters there.

The *tropicalis*-form appears to be restricted to waters relatively close to shore, much like *D. capensis capensis* (see below). There are no records from oceanic waters far from shore in the Indian Ocean, despite recent marine mammal survey effort in several such areas (Keller *et al.* 1982, Leatherwood *et al.* 1984, Corbett 1994, Eyre 1995, Ballance and Pitman 1998, de Boer 2000). Nor are there any confirmed records from oceanic island groups such as the Seychelles (Keller *et al.* 1982, Racey and Nicoll 1984), Maldives[8] (Anderson *et al.* 1999), Andaman/Nicobar Islands,[9] and Mauritius/Reunion (Corbett 1994), despite a number of recent records of sightings and strandings of many other species of cetaceans in these areas. Also, no records have been obtained from the Philippines (this archipelago

[5] Personal communication from V. G. Cockcroft, Centre for Dolphin Stuides, Box 1856, Plettenberg Bay 6600, South Africa, May 2001.

[6] Personal communication from I. Beasley, Tropical Environment Studies and Geography, James Cook University, Townsville, Queensland 4811, Australia, April 2001.

[7] Lekagul and McNeely (1988) reported several records for the Gulf of Thailand, but at least some of these are erroneous. The skull photos in their book, supposedly of *Delphinus*, are actually of a species of *Stenella*.

[8] Deranayagala (1956) did report a skull of a common dolphin from the Maldives, but Anderson *et al.* (1999) considered the record and species identification unreliable. Due to a lack of information on how the skull was identified, we agree with Anderson *et al.* (1999).

[9] Sivaprakasam (1980) presented a report of a common dolphin taken on a tuna longline at the Andaman Islands. Again, because there was no information presented on how the identification was made, we consider this record to be unconfirmed.

is mostly surrounded by deep, oceanic waters), even though this area has been surveyed extensively in recent years (Dolar and Wood 1993, Dolar and Perrin 1996, Dolar *et al.* 1997). Finally, the only report of *Delphinus* around Madagascar appears to be the type specimen of *Delphinus sao* Gray, 1846, the correct species identification of which is not known (see Appendix III).

Alling (1986) reported that 57% of the groups she observed were in waters greater than 1,000 m deep. Ballance and Pitman (1998) made all their sightings in a localized area off the coast of Oman, in waters ranging from 89 to 1,157 m deep (mean = 720.2 ± 278.41 m SD, $n = 14$), but generally near shallow waters. These animals have been reported to prefer "deep" waters of the Oman Sea (presumably the Gulf of Oman or Arabian Sea, Pilleri and Gihr 1974), off Saudi Arabia (Robineau and Fiquet 1994), and in the Persian Gulf (Henningsen and Constantine 1992), which is predominantly shallow. However, Robineau and Fiquet (1996) clarified that their sightings off Saudi Arabia were in waters only 10–30 m deep. Sightings reported by Small and Small (1991) off Somalia were in waters 16–148 m deep, and those by Leatherwood *et al.* (1984) from the Strait of Malacca and Andaman Sea were in waters less than 100 m deep. A recent sighting off Cambodia in the Gulf of Thailand was in waters 45 m deep (footnote 6), and sightings from Hong Kong in recent years have all been in waters less than 40 m deep (TAJ, unpublished data). Therefore, it appears that the *tropicalis*-form may be largely a species of the continental shelf and slope. Water temperatures in areas where these animals were sighted off Saudi Arabia were 19–20°C (Robineau and Fiquet 1996). Additional information on the biology of this subspecies is reviewed in Appendix IV.

Suggested common name—Because it is apparently the only form of common dolphin in the tropical and subtropical Indo-Pacific area, we suggest the common name "Indo-Pacific common dolphin" for *D. capensis tropicalis*.

Redescription of Delphinus capensis capensis *Gray, 1828*

Delphinus capensis Gray, 1828—Type locality Cape of Good Hope (BMNH 41. 17.34, whole mount with skull).
Delphinus major Gray, 1866—Type locality unknown (BMNH 1852.10.5.2, skull).
Delphinus moorei Gray, 1866—Type locality southwest of the Cape of Good Hope (Liverpool Free Museum, skull).
Delphinus microps Burmeister, 1866 (not *D. microps* Gray, 1846)—Type locality off the coast of Brazil (three syntype skulls).
Delphinus bairdii Dall, 1873—Type locality off Point Arguello, California (2 syntypes, specimens apparently lost).

Holotype and type locality—The type specimen is a whole mount with skull stored at the Natural History Museum, London (formerly the British Museum of Natural History). The specimen is registered with the number BMNH 41.17.34. It was collected in the 19th Century by Captain Heaviside (Haviside) off the Cape of Good Hope, South Africa.

Diagnosis—Delphinus capensis capensis is characterized by a color pattern that is less boldly patterned and more muted that in *D. delphis* (the description below is adapted from Heyning and Perrin 1994, which is based largely on specimens from Californian waters). The typical *Delphinus* "hourglass" pattern occurs in the lateral area of the body, but the margin between the dark cape and light thoracic

patch is generally less distinct and has less contrast than in *D. delphis*. The whiteness of the ventral area rarely extends above the level of the flipper stripe. Compared to *D. delphis*, the flipper-to-anus stripe is more developed, the flipper stripe narrows less as it extends forward and is wider and often contacts the lip patch near the gape, the eye patch has less contrast with the thoracic patch, and there is less evidence of light-colored patches on the flippers and dorsal fin.

The body is generally more slender than in *D. delphis*, and the profile of the melon is flatter and it rises at a shallower angle from the beak (Heyning and Perrin 1994). The beak is long, on average longer than in *D. delphis*, but shorter than in *D. capensis tropicalis* (about 6.9%–7.6% of total body length; Heyning and Perrin 1994) Total length of adult females ranges from 193 to 222 cm, and adult males from 202 to 254 cm (Heyning and Perrin 1994). Good photos of the external appearance can be found in Heyning and Perrin (1994).

The skull of adults ranges from 449 to 541 mm condylobasal length, and is much wider, with a shorter rostrum than in *D. capensis tropicalis*; the rostral length/zygomatic width ratio is 1.46–1.77 (Amaha 1995, this study). Tooth counts are on average lower than in the Indo-Pacific subspecies, with upper tooth counts of 47–60 and lower tooth counts of 47–57 (Heyning and Perrin 1994). Amaha (1995) reported maximum tooth counts as high as 62 for eastern North Pacific specimens. The mandibular symphysis is shorter on average than in *D. capensis tropicalis*; it ranges from 44 to 85 mm in length (Amaha 1995). The vertebral formula is C7, T14, L18–23, Ca30–37, for a total of 72–80 vertebrae (Heyning and Perrin 1994).

Geographic variation—Color pattern information has not been well documented for most populations of the subspecies, but Amaha (1995) stated that the Japanese long-beaked population does not show the wide flipper stripe characteristic of the long-beaked stock(s) in the eastern North Pacific. There is some evidence that both body length and beak length may be greater on average in South Africa than in the eastern North Pacific (Heyning and Perrin 1994).

Tooth counts for South African specimens are slightly lower than those from Japan and the eastern North Pacific (Fig. 2). Peruvian specimens also appear to have lower tooth counts than animals from the latter two areas (Amaha 1995). The populations of the eastern North Pacific and Peru may have lower rostral length/zygomatic width ratios than those from Japan or South Africa (Amaha 1995). Vertebral counts of specimens from South Africa (72–76) are lower than those of specimens from the eastern North Pacific (77–80) (Heyning and Perrin 1994).

Distribution and habitat—This subspecies is known from five more-or-less discrete areas in the Atlantic and Pacific oceans, and one area in the southwestern Indian Ocean (off southern Africa). Long-beaked common dolphins apparently have an extensive distribution along the east coast of South America, extending from at least Venezuela south to Argentina (Casinos 1984, Heyning and Perrin 1994). Along the west coast of Africa, common dolphins also have an extensive distribution (Cadenat 1959, Jefferson *et al.* 1997), and *D. capensis* has been confirmed to occur from at least Gabon to Angola and Senegal.[10] There are one or

[10] Van Waerebeek, K. 1997. Long-beaked and short-beaked common dolphins sympatric off central-west Africa. International Whaling Commission Scientific Committee Report SC/49/SM46 (unpublished). Available from the International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge CB4 9NP, U.K.

more long-beaked common dolphin populations off southern Japan and Korea (Schlegel 1844; Ogawa 1936; Okada and Hanaoka 1938; Takemura *et al.* 1967; Amaha 1995; TAJ, unpublished data). The distribution may extend into Chinese waters of the Yellow and Bohai seas (Wang 1979, Shi and Wang 1983, Zhou *et al.* 1995), although the taxonomic affiliations of these common dolphins have not yet been confirmed.[11] The best-studied stock of *D. capensis* is in the eastern North Pacific, where it ranges from at least central California south to Baja California, Mexico (including the entire Gulf of California) (Dizon *et al.* 1994, Heyning and Perrin 1994). There is an apparently isolated population of long-beaked common dolphins off the coast of Peru (KVW, unpublished data). The only place in the Indian Ocean in which *D. capensis capensis* is known to occur is off the coast of South Africa (Ross 1984, Cockcroft and Peddemors 1990, Findlay *et al.* 1992, Peddemors 1999), and this stock may also extend northward along the poorly studied coast of central East Africa. Common dolphins that may be affiliated with this stock have been observed in Mozambique and Kenya (footnote 5).

Delphinus capensis capensis is found in nearshore tropical to warm temperate waters. It appears to be largely restricted to waters over and near the continental shelf. In the eastern North Pacific, off California and Baja California, Mexico, it occurs mostly within 184 km of the coast (Perrin *et al.* 1985, Dizon *et al.* 1994). In the eastern Pacific, common dolphins (species unidentified) prefer areas with large seasonal changes in surface temperature and thermocline depth, and seasonal upwelling (Au and Perryman 1985), and at least off southern California they also prefer areas over undersea seamounts (Evans 1975, 1982). In southern Africa, they are also relatively coastal, although they may occur in warmer and deeper waters along the west coast than the east (Findlay *et al.* 1992, Peddemors 1999). Off the KwaZulu/Natal coast, they occur only inshore in the austral winter, during the annual "sardine run" (Ross 1984, Cockcroft and Peddemors 1990).

Suggested common name—Because it is the form of long-beaked common dolphin that is most commonly encountered in the Pacific and Atlantic oceans and the more familiar to most people, we suggest the name "long-beaked common dolphin" for *D. capensis capensis*.

Conclusions

We conclude that the *tropicalis*-form common dolphin is probably an extremely long-beaked subspecies of *D. capensis*, which may hybridize or intergrade with the ordinary form *D. capensis* where the two overlap in distribution along the coast of east Africa and in southeast Asia. *Delphinus capensis tropicalis* (van Bree, 1971) is largely a continental shelf and slope form and it does not appear to be found in deep, offshore waters, nor around oceanic islands in the Indo-Pacific.

There are several possible scenarios that could account for the evolution of these subspecies. We think it is possible that at some point in the Pleistocene, long-beaked common dolphins in the Indian Ocean became isolated from other

[11] We measured four *Delphinus* specimens from Putian, cental China (CKU PT-97-02, PT-97-03, PT-97-04, PT-97-05) that did not seem to fit in with the *tropicalis* specimens measured from other parts of the Chinese coast. These specimens were considered unidentified to subspecies. They probably represent *D. c. capensis* specimens, or may even be intermediates.

such groups in the Pacific and Atlantic oceans. This may have occurred during periods of extremely low sea levels, such as those that occurred about 18,000 and 130,000 yr ago. This would have caused the geographic isolation necessary to set in motion the process of genetic isolation. However, if the isolation was not sustained as sea levels again rose, these groups could have come back into contact near the eastern and western margins of the Indian Ocean. If speciation had not been complete, then it is likely that recontact would have resulted in some level of hybridization where the two subspecies are now parapatric. This would explain the pattern of morphological variation that we have found in this study.

However, this is only one possibility. In the only available study of the genetic relationships of the *tropicalis* form, the single *tropicalis* sample of LeDuc *et al.* (1999) occupied a position basal within the genus. However, their study examined only one gene (cytochrome *b*) and the sample size was small (two short-beaked, two eastern Pacific long-beaked, and one *tropicalis*-type samples), and as pointed-out by Milinkovitch *et al.* (2002), conclusions should therefore be viewed with caution. In any event, we believe the results of our study provide evidence that the *tropicalis*-form is not a separate species of common dolphin.

If the results of LeDuc *et al.* (1999) and of the current study are both accurate, then the long-beaked common dolphins in the eastern Pacific would not be conspecific with the Indo-Pacific *D. capensis* (see Milinkovitch *et al.* 2002). In this case, *Delphinus bairdii* Dall, 1873 would apply (or less likely *Delphinus microps* Burmeister, 1866), and the genus *Delphinus* would contain at least three species. The importance and urgency of resolving this taxonomic problem thus becomes even more apparent. In the future, examination of appropriate samples to determine molecular genetic diversity among the forms will surely provide additional clues to their origins and systematic relationships.

Acknowledgments

We would like to thank many people for their assistance with this project. First, the museum curators and their assistants who kindly allowed us access to specimens under their care: P. Best (ZAM), P. J. H. van Bree and D. Kreb (ZMA), R. Chen (OW), S. T. Chen (CKU), Y. J. Chen (NMNS), L. M. Chou (ZRC), V. G. Cockcroft and W. Kant (PEM), T. Ennis (AM), M. Gallagher, S. Rhomadan Al Lawati and S. Mustafa Al Lawati (ONHM), M. Gavanol (BNHS), J. E. Heyning and D. Janiger (LACM), Dao Tan Ho (WT CB, WT VL), P. Jenkins and R. Sabin (BMNH), C. Kemper (SAM), R. S. Lal Mohan (RSLM), J. G. Mead (USNM), D. Moerike (SMNS), W. F. Perrin (SWFSC), D. Robineau (MNHN), C. Smeenk (RMNH), T. Yamada (NSMT), C. Yang (ZRC), and K. Zhou and G. Yang (NJNU). Second, the many helpers and assistants who played a part in collection of the data. Third, our colleagues who generously provided unpublished information. Discussions and correspondence with several people, in particular A. Amaha, P. Best, P. J. H. van Bree, R. L. Brownell Jr., V. G. Cockcroft, J. E. Heyning, W. F. Perrin, D. Robineau, and C. Smeenk, were extremely helpful to us in the formulation of the ideas presented in this paper. Much of the data for this project were collected incidentally during the course of studies on Hong Kong dolphins and porpoises funded by the Agriculture, Fisheries and Conservation Department of the Hong Kong SAR Government. Comments by J. E. Heyning, W. F. Perrin, and D. W. Rice greatly improved the manuscript. Fig. 1 was drafted by H. Orr. To all of these individuals and institutions, we are very grateful.

Literature Cited

Alling, A. 1986. Records of odontocetes in the northern Indian Ocean (1981–1982) and off the coast of Sri Lanka (1982–1984). Journal of the Bombay Natural History Society 83:376–394.

Amaha, A. 1995. Geographic variation of the common dolphin, *Delphinus delphis* (Odontoceti: Delphinidae). Ph.D. thesis, Tokyo University of Fisheries, 211 pp.

Anderson, R. C., A. Shaan and Z. Waheed. 1999. Records of cetacean 'strandings' from the Maldives. Journal of South Asian Natural History 4:187–202.

Au, D. W. K., and W. L. Perryman. 1985. Dolphin habitats in the eastern tropical Pacific. Fishery Bulletin, U.S. 83:623–643.

Baldwin, R., and R. Salm. 1994. Whales and dolphins along the coast of Oman. Published privately by Robert Baldwin.

Baldwin, R., K. Van Waerebeek and M. Gallagher. 1998. A review of small cetaceans from waters of the Arabian Peninsula. International Whaling Commission, Scientific Committee Report SC/50/SM6 (unpublished report). Available from The International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge CB4 9NP, U.K..

Ballance, L. T., and R. L. Pitman. 1998. Cetaceans of the western tropical Indian Ocean: Distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. Marine Mammal Science 14:429–459.

Blanford, W. T. 1888. The fauna of British India including Ceylon and Burma. Taylor and Francis, London.

Blyth, E. 1859. On the great rorqual of the Indian Ocean, with notices of other cetals and of the syrenia or marine pachyderms. Journal of the Asiatic Society of Bengal 28:481–495.

de Boer, M. N. 2000. A note on cetacean observations in the Indian Ocean Sanctuary and the South China Sea, Mauritius to the Philippines, April 1999. Journal of Cetacean Research and Management 2:197–200.

van Bree, P. J. H. 1971*a*. *Delphinus tropicalis*, a new name for *Delphinus longirostris* G. Cuvier, 1829. Mammalia 35:345–346.

van Bree, P. J. H. 1971*b*. On two skulls of *Delphinus dussumieri* Blanford, 1891 (Notes on Cetacea, Delphinoidea I). Beaufortia 237:169–172.

van Bree, P. J. H., and M. D. Gallagher. 1978. On the taxonomic status of *Delphinus tropicalis* van Bree, 1971. (Notes on Cetacea, Delphinoidea IX). Beaufortia 28:1–8.

Burmeister, H. 1866. On some cetaceans. Annals and Magazine of Natural History 18:99–103.

Cadenat, J. 1959. Rapport sur les petits cetaces ouest-africains. Resultats des recherches enterprises sur ces animaux jusqu'au mois de mars 1959. Bulletin de l'Institut Francais Afrique Noire 21A:1367–1409.

Casinos, A. 1984. A note on the common dolphin of the South American Atlantic coast, with some remarks about the speciation of the genus *Delphinus*. Acta Zoologica Fennica 172:141–142.

Chantrapornsyl, S., K. Adulyanuksol and K. Kittiwathanawong. 1996. Records of cetaceans in Thailand. Phuket Marine Biological Center Research Bulletin 61:39–63.

Corbett, H. D. 1994. The occurrence of cetaceans off Mauritius and in adjacent waters. Report of the International Whaling Commission 44:393–397.

Cockcroft, V. G., and V. M. Peddemors. 1990. Seasonal distribution and density of common dolphins *Delphinus delphis* of the south-east coast of southern Africa. South African Journal of Marine Science 9:371–377.

Cuvier, G. 1829. Le règne animal distribue d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée. Chez Deterville, Libraire.

Dall, W. H. 1873. Descriptions of three new species of Cetacea, from the coast of California. Proceedings of the California Academy of Sciences 5:12–14.

DERANIYAGALA, P. E. P. 1956. Zoological collecting at the Maldives in 1932. Spolia Zeylanica 28:7–16.

DIZON, A. E., W. F. PERRIN AND P. A. AKIN. 1994. Stocks of dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific: A phylogeographic classification. NOAA Technical Memorandum NMFS 119. 20 pp.

DOLAR, M. L. L., AND W. F. PERRIN. 1996. Preliminary results of the distribution and abundance of cetaceans in the Philippines. IBI Reports 6:9–24.

DOLAR, M. L. L., AND C. J. WOOD. 1993. Survey of marine mammals in the central Visayas and northern Mindanao. Enviroscope 7:1–7.

DOLAR, M. L. L., W. F. PERRIN, A. A. S. P. YAPTINCHAY, S. A. B. H. J. JAAMAN, M. D. SANTOS, M. N. ALAVA AND M. S. B. SULIANSA. 1997. Preliminary investigation of marine mammal distribution, abundance, and interactions with humans in the southern Sulu Sea. Asian Marine Biology 14:61–81.

EVANS, W. E. 1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linneaus in the northeastern Pacific. Ph.D. thesis, University of California, Los Angeles, CA. 145 pp.

EVANS, W. E. 1982. Distribution and differentiation of stocks of *Delphinus delphis* Linneaus in the northeastern Pacific. Pages 45–66 *in* Mammals in the seas. FAO Fisheries Series No. 5, Volume IV. Food and Agriculure Organization of the United Nations.

EVANS, W. E. 1994. Common dolphin, white-bellied porpoise *Delphinus delphis* Linneaus, 1758. Pages 191–224 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals, Volume 5. The first book of dolphins. Academic Press, London.

EYRE, E. J. 1995. Obervations of cetaceans in the Indian Ocean Whale Sanctuary, May–July, 1993. Report of the International Whaling Commission 45:419–426.

FINDLAY, K. P., P. B. BEST, G. J. B. ROSS AND V. G. COCKCROFT. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. South African Journal of Marine Science 12:237–270.

FISCHER, J. B. 1829. Synopsis mammalium. J. G. Cotta, Stuttgart, Germany.

FLOWER, W. H. 1883. On the characters and divisions of the family Delphinidae. Proceedings of the Zoological Society of London 1883:466–513.

GALLAGHER, M. D. 1991. Collection of skulls of Cetacea: Odontoceti from Bahrain, United Arab Emirates and Oman, 1969–1990. UNEP Marine Mammal Technical Report 3:89–97.

GAO, G., AND K. ZHOU. 1991. The number of fibers and range of fiber diameters in the cochlear nerve of three odontocete species. Canadian Journal of Zoology 69:2360–2364.

GAO, G., AND K. ZHOU. 1992. Fiber analysis of the optic and cochlear nerves of small cetaceans. Pages 39–52 *in* J. Thomas, R. Kastelein and A. Supin, eds. Marine mammal sensory systems. Plenum Press, New York, NY.

GIBSON-HILL, C. A. 1949. The whales, porpoises and dolphins known in Malayan waters. Malayan Nature Journal 4:44–61.

GIBSON-HILL, C. A. 1950. The whales, porpoises and dolphins known in Sarawak waters. Sarawak Museum Journal 5:288–296.

GRAY, J. E. 1828. Spicilegia Zoologica; or original figures and short systematic descriptions of new and unfigured animals. Treuttel, Wurtz and Co.

GRAY, J. E. 1846. On the cetaceous animals. Pages 13–53 *in* J. Richardson and J. E. Gray, eds. The zoology of the voyage of H.M.S. Erebus and Terror, under the command of Captain Sir James Clark Ross, R.N., FR.S., during the years 1839 to 1843. Volume 1: Mammalia, birds. E. W. Janson, London.

GRAY, J. E. 1866. Description of three species of dolphins in the Free Museum at Liverpool. Proceedings of the Zoological Society of London 1865:735–739.

HAMSA, K. M. S. A., AND P. NAMMALWAR. 1978. Description of isopod *Cirolana parva* Hansen parasitic on the eye balls of dolphin, *Delphinus delphis* Linneaus with a key to the Indian species of the genus *Cirolana* Leach. Journal of the Bombay Natural History Society 75:516–519.

HENNINGSEN, T., AND R. CONSTANTINE. 1992. Cetaceans in the Persian Gulf: After the war. European Research on Cetaceans 6:108–113.

HERSHKOVITZ, P. 1966. Catalog of living whales. Bulletin of the United States National Museum 246. 259 pp.

HEYNING, J. E., AND W. F. PERRIN. 1994. Evidence for two species of common dolphins (genus *Delphinus*) from the eastern North Pacific. Natural History Museum of Los Angeles County, Contributions in Science 442. 35 pp.

ILANGAKOON, A. 1997. Species composition, seasonal variation, sex ratio and body length of small cetaceans caught off west, south-west and south coast of Sri Lanka. Journal of the Bombay Natural History Society 94:298–306.

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE). 1999. The International code of zoological nomenclature. Fourth Edition. International Trust for Zoological Nomenclature, London.

JAMES, P. S. B. R., AND R. S. LAL MOHAN. 1987. The marine mammals of India. Marine Fisheries Information Service 71:1–14.

JAMES, P. S. B. R., A. P. LIPTON, J. P. KARBARI, M. MOHAN, R. S. LAL MOHAN, M. S. RAJAGOPALAN, G. GOPAKUMAR, M. E. RAJAPANDIAN, S. KRISHNA PILLAI, M. SIVADAS, P. NAMMALWAR AND G. RADHAKRISHNAN. 1987. Investigations on whales, dolphins and dugongs (FB/PR/14). Central Marine Fisheries Research Institute, Cochin. Annual Report 1986-87:29–30.

JAYAPRAKESH, A. A., P. NAMMALWAR, S. KRISHNA PILLAI AND M. N. K. ELAYATH. 1995. Incidental by-catch of dolphins at Fisheries Harbour, Cochin with a note on their conservation and management in India. Journal of the Marine Biological Association of India 37:126–133.

JEFFERSON, T. A., B. E. CURRY, S. LEATHERWOOD AND J. A. POWELL. 1997. Dolphins and porpoises of West Africa: A review of records (Cetacea: Delphinidae, Phocoenidae). Mammalia 61:87–108.

KELLER, R. W., S. LEATHERWOOD AND S. J. HOLT. 1982. Indian Ocean cetacean survey, Seychelle Islands, April through June 1980. Report of the International Whaling Commission 32:503–515.

KRISHNA PILLAI, S., AND A. P. LIPTON. 1996. Dolphin killed by the propeller of a trawler. Central Marine Fisheries Information Service, Technical and Extension Series 141:18.

LAL MOHAN, R. S. 1983. Taxonomic position of the dolphin, *Delphinus longirostris* Cuvier. Unpublished report. Available from the author: Conservation of Nature Trust, Lagrace, 43-C, Water Tank Road, Nagercoil 629 001, Tamil Nadu, India.

LAL MOHAN, R. S. 1985*a*. Osteology of dolphins, *Delphinus delphis tropicalis*, *Stenella longirostris*, *Tursiops aduncus* and *Sousa chinensis* from south-west coast of India. Proceedings of the Symposium on Endangered Marine Animals and Marine Parks 1:93–99.

LAL MOHAN, R. S. 1985*b*. Observations of the by-catch of dolphins *Stenella longirostris*, *Tursiops aduncus*, *Sousa chinensis* and *Delphinus delphis tropicalis* in the gill nets off Calicut coast, India. Proceedings of the Symposium on Endangered Marine Animals and Marine Parks 1:78–83.

LAL MOHAN, R. S. 1994. Review of gillnet fisheries and cetacean bycatches in the northeastern Indian Ocean. Reports of the International Whaling Commission (Special Issue 15):329–346.

LAL MOHAN, R. S. 1995. Age determination of dolphins entangled in gillnets along the Kerala coast. Journal of the Bombay Natural History Society 92:77–80.

LEATHERWOOD, S., AND R. R. REEVES. 1989. Marine mammal research and conservation in Sri Lanka 1985–1986. UNEP Marine Mammal Technical Report 1. 138 pp.

LEATHERWOOD, S., C. B. PETERS, R. SANTERRE, M. SANTERRE AND J. T. CLARKE. 1984. Observations of cetaceans in the northern Indian Ocean Sanctuary, November 1980–May 1983. Report of the International Whaling Commission 34:509–520.

LEDUC, R. G., W. F. PERRIN AND A. E. DIZON. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome *b* sequences. Marine Mammal Science 15:619–648.

LEKAGUL, B., AND J. A. MCNEELY. 1988. Mammals of Thailand (Second Edition). Darnsutha Press, Bangkok.

LEWIN, H. G. D. 1958. Dolphins in the South China Sea. Malayan Nature Journal 12:158–160.

MAHADEVAN PILLAI, P. K., AND S. B. CHANDRANGATHAN. 1990. On the drift net-entangled dolphins landed at Sakthikulangara. Central Marine Fisheries Information Service, Technical and Extension Series 104:16–17.

MILINKOVITCH, M. C., R. LEDUC, R. TIEDEMANN AND A. E. DIZON. 2002. Applications of molecular data in cetacean taxonomy and population genetics with special emphasis on defining species boundaries. Pages 325–359 *in* P. G. H. Evans and J. A. Raga, eds. Marine mammals: Biology and conservation. Kluwer Academic/Plenum Publishers, Dordrecht, The Netherlands.

OGAWA, T. 1936. Studien uber die zahnwale in Japan. (I. Mitteilung). Syokubutu Oyobi Dobutu, Tokyo (Botany and Zoology) 4(7):1–13 (in Japanese).

OKADA, Y., AND T. HANAOKA. 1938. A study of Japanese Delphinidae (II). *Delphinus delphis* Linneaus. "Mairuka". Scientific Reports of the Tokyo Bunrika Daigaku 3:243–272.

OWEN, R. 1866. On some Indian Cetacea collected by Walter Elliot, Esq. Transactions of the Zoological Society of London 6:17–47.

PARSONS, E. C. M., M. L. FELLEY AND L. J. PORTER. 1995. An annotated checklist of cetaceans recorded from Hong Kong's territorial waters. Asian Marine Biology 12:79–100.

PEDDEMORS, V. M. 1999. Delphinids of southern Africa: A review of their distribution, status and life history. Journal of Cetacean Research and Management 1:157–165.

PERRIN, W. F. 1975. Variation and taxonomy of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. Bulletin of the Scripps Institution of Oceanography 21. 206 pp.

PERRIN, W. F. 1998. *Stenella longirostris*. Mammalian Species 599:1–7.

PERRIN, W. F., AND J. E. HEYNING. 1993. Rostral fusion as a criterion of cranial maturity in the common dolphin, *Delphinus delphis*. Marine Mammal Science 9:195–197.

PERRIN, W. F., M. D. SCOTT, G. J. WALKER AND V. L. CASS. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA Technical Report NMFS 28. 28 pp.

PILLERI, G. 1974. First record of *Anisakis typica* (Nematoda, Ascaridata) in *Delphinus tropicalis* and *Neophocaena phocaenoides* off the coast of Pakistan. Investigations on Cetacea 5:339–340.

PILLERI, G., AND M. GIHR. 1972*a*. Contribution to the knowledge of the cetaceans of Pakistan with particular reference to the genera *Neomeris*, *Sousa*, *Delphinus* and *Tursiops* and description of a new Chinese porpoise (*Neomeris asiaorientalis*). Investigations on Cetacea 4:107–162.

PILLERI, G., AND M. GIHR. 1972*b*. A rare species of dolphin *Delphinus tropicalis* van Bree, 1971 (=*dussumieri* Blanford, 1891) from the coast of Pakistan. Mammalia 36:406–413.

PILLERI, G., AND M. GIHR. 1974. Contribution to the knowledge of the cetaceans of southwest and monsoon Asia (Persian Gulf, Indus Delta, Malabar, Andaman Sea and Gulf of Siam). Investigations on Cetacea 5:95–150.

RACEY, P. A., AND M. E. NICOLL. 1984. Mammals of the Seychelles. Pages 607–626 *in* D. R. Stoddart, ed. Ecology and biogeography of the Seychelles Islands. Dr. W. Junk, Dordrecht, The Netherlands.

RICE, D. W. 1977. A list of the marine mammals of the world. NOAA Technical Report NMFS SSRF 711. 15 pp.

RICE, D. W. 1998. Marine mammals of the world: Systematics and distribution. Special Publication Number 4. Society for Marine Mammalogy, Lawrence, KS.

ROBINEAU, D. 1990. Les types de cetaces actuels du Muséum national d'Histoire naturelle II. Delphinidae, Phocoenidae. Bulletin de Muséum National d'Histoire Naturelle, Paris 12:197–238.

ROBINEAU, D., AND P. FIQUET. 1994. Cetaceans of Dawhat ad-Dafi and Dawhat al-Musallamiya (Saudi Arabia) one year after the Gulf War oil spill. Courier Forschungsinstitut Senckenberg 166:76–80.

ROBINEAU, D., AND P. FIQUET. 1996. The Cetacea of the Jubail Marine Wildlife Sanctuary, Saudi Arabia. Pages 438–458 *in* F. Krupp, A. H. Abuzinada and I. A. Nader, ed. A marine wildlife sanctuary for the Arabian Gulf. Environmental research and conservation following the 1991 Gulf War oil spill. National Commission for Wildlife Conservation and Development, Riyadh and Senckenberg Research Institute, Frankfurt.

ROBINEAU, D., AND J. M. ROSE. 1984. Les cetaces de Djibouti. Bilan de connaissances actuelles sur la faune cetologique de la mer Rouge et de Golfe d'Aden. Bulletin de Museum National d'Histoire Naturelle, Paris 6:219–249.

ROSEL, P. E., A. E. DIZON AND J. E. HEYNING. 1994. Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). Marine Biology 119:159–167.

ROSS, G. J. B. 1984. The smaller cetaceans of the south east coast of southern Africa. Annals of the Cape Provincial Museums (Natural History) 15:173–410.

SALM, R. V. 1992. Impact of fisheries in environment and wildlife Sultanate of Oman. Unpublished report. Available from the author: IUCN Coastal Zone Management Project, Rue Mauverney 28, Gland 1196, Switzerland.

SALM, R. V., R. A. C. JENSEN AND V. A. PAPASTAVROU. 1993. Marine fauna of Oman: Cetaceans, turtles, seabirds and shallow water corals. Marine Conservation and Development Report. IUCN, Gland, Switzerland.

SCHLEGEL, H. 1844. Les cetaces. Pages 13–16 *in* C. J. Temminck and H. Schlegel, eds. Fauna Japonica. Lugduni Batavorum.

SCLATER, W. L. 1981. Catalogue of Mammalia preserved in the Indian Museum Calcutta. Cosmo Publications, New Delhi, India.

SHI, Y., AND X. WANG. 1983. The toothed whales in the offshore of Liaoning Province. Transactions of Liaoning Zoological Society 12:83–87. (in Chinese)

SIGURDSSON, J. B., AND C. M. YANG. 1990. Marine mammals of Singapore. Pages 25–37 *in* L. M. Chou and P. K. L. Ng, eds. Essays in zoology. National University of Singapore.

SIVAPRAKASAM, T. E. 1980. On the unusual occurrence of the common dolphin, *Delphinus delphis* Linneaus in longline catches at Port Blair, Andamans. Journal of the Bombay Natural History Society 77:320–321.

SMALL, J. A., AND G. J. SMALL. 1991. Cetacean observations from the Somali Democratic Republic, September 1985 through May 1987. UNEP Marine Mammal Technical Report 3:179–210.

SMEENK, C., M. J. ADDINK, A. B. VAN DER BERG, C. A. W. BOSMAN AND G. C. CADEE. 1996. Sightings of *Delphinus* cf. *tropicalis* van Bree, 1971 in the Red Sea. Bonner Zoologische Beitrage 46:389–398.

SMITH, B. D., T. A. JEFFERSON, D. T. HO, S. LEATHERWOOD, C. V. THUOC, M. ANDERSEN AND E. CHIAM. 1995. Marine mammals of Vietnam: A preliminary checklist. Tuyen Tap Nghien Cuu Bien (Collection of Marine Research Works) 6:147–176.

SMITH, B. D., T. A. JEFFERSON, S. LEATHERWOOD, D. T. HO, C. V. THUOC AND L. H. QUANG. 1997. Investigations of marine mammals in Vietnam. Asian Marine Biology 14:145–172.

TAKEMURA, A., K. YOSHIDA AND K. MIZUE. 1967. Studies on the little toothed whales in the west sea area of Kyushu-XIV. Hase iruka (Hase dolphin) caught in the south sea area of Saishu Is. in the East China Sea. Bulletin of the Faculty of Fisheries, Nagasaki University 24:39–53.

TRUE, F. W. 1889. Contributions to the natural history of the cetaceans, a review of the family Delphinidae. Bulletin of the United States National Museum 36. 191 pp.

VAN WAEREBEEK, K., M. GALLAGHER, R. BALDWIN, V. PAPASTAVROU AND M. AL-LAWATI-SAMIRA. 1999. Morphology and distribution of the spinner dolphin, *Stenella longirostris*,

rough-toothed dolphin, *Steno bredanensis*, AND melon-headed whale, *Peponocephala* electra, from waters off the Sultanate of Oman. Journal of Cetacean Research and Management 1:167–178.

WANG, P. 1979. A survey of medium and small sizes toothed whales in Bohai and Yellow Sea. Chinese Journal of Zoology 5:31–34. (in Chinese)

WANG, P. 1984. Distribution of cetaceans off the coast of China. Chinese Journal of Zoology 6:52–56. (in Chinese)

WANG, P. 1985 (1984). Distribution of cetaceans in Chinese waters. Southwest Fisheries Center Administrative Report LJ-85-24. 11 pp.

WANG, P. 1990. Cetaceans in the coast of Guangxi. Guangxi Fisheries Science and Technology 3:1–6. (in Chinese)

WHITE, C. 1999. Molecular systematics of the common dolphin, *Delphinus delphis*. B.Sc. thesis, University of Adelaide, Australia. (not seen)

YANG, H. C. 1976. Studies on the whales, porpoises and dolphins of Taiwan. Annual Report of Science, Taiwan Museum 19:131–178.

ZHOU, K., Y. LI, W. QIAN AND G. YANG. 1980. Notes on three species of dolphins from the South China Sea and Jiulongjiang River. Oceanologica et Limnologica Sinica 11:306–313. (in Chinese, with English summary)

ZHOU, K., S. LEATHERWOOD AND T. A. JEFFERSON. 1995. Records of small cetaceans in Chinese waters: A review. Asian Marine Biology 12:119–139.

Received: 27 June 2001
Accepted: 8 April 2002

APPENDIX I

SPECIMENS EXAMINED

Delphinus capensis tropicalis—AM M22899; BMNH 73.1746, 1949.7.15.4, 1954.9.9.2, 1965.12.17.1, 1973.108, 1981.711, 1995.55; BNHS M5964, UN-44; MNHN A-3065 (*D. tropicalis* holotype), 1981.161, 1993–86, 1993–87; NJNU 0058-8314, 0061-8121, 0062-8122, 0341-9052, 7601, 7602, 7902, 7912, 8314, 8726; NMNS 1290; NSMT 24780; ONMH no #, 428, 429, 564, 836, 863, 873, 1137, 1140, 1368, 1390–1392, 1394, 1490, 1518, 1562, 1566–1568, 1678, 2572; OW no #; RSLM no # ($n = 5$), 1670, A3; SMNS 45762, 45765, 47566, 45768, 45771, PT475, PT489, PT590, PT492, PT493; SWFSC WFP 813; USNM 49977, 550963, 550974–550980; WT CB1; WT VL5; WT VT17; ZMA 16.995, 20.294, 20.321, 20.322, 20.898, 21.169.

Delphinus capensis capensis—BMNH 1852.10.5.2 (*D. major* holotype), 41.17.34 (*D. capensis* holotype); LACM 54618, 72429, 72430, 72469, 72494, 72502, 72593, 84021, 86004, 88902, 88979, 88982, 88997, 90277, 91303, 91762, 91770, 91303, 91762, 91770, 91780, 91890, 91940, 91951, 91959, 91962, 92067, 92071, 92077, 95668, 95716; NSMT no #, 5099, 5633, 23717–23721, 23723–23726, 24826, 26401, 26612, 26613, 27722, 28350, 29636; PEM N549, N972, N1755, N1813, N1823, N1842, N1846, N1850–1851, N1853, N1902, N1904–1905, N1914–1915, N1926, N2098, N2100–2101, N2103–2105, N2275, N2278, N2338, N2429, N2436, N2670, N2681, N2684, N2734, N2783; SWFSC 0039, 0043, WFP 521; USNM 22881, 550938; ZAM 39872, 39950, 40605, 40608, 40927, 41102, 41192.

Delphinus capensis (unidentified subspecies)—BMNH 1866.2.5.5 (*D. pomeegra* holotype); CKU PT-97-02, PT-97-03, PT-97-04, PT-97-05; OPCF UD97-8/8.

Delphinus delphis—AM 52065, M12400, M12407, M140, M26999, M27971, M33618, S1912, S276; BMNH 1869.8.11.1; QM J2776, JM2033, JM2094; SAM M12797, 16969, M18042, M18907, M19961, M19980, M19982, M19983, M19986.

APPENDIX II

MUSEUM AND COLLECTION ACRONYMS

AM, Australian Museum, Sydney, Australia; BMNH, British Museum (Natural History), London, U.K.; BNHS, Bombay Natural History Society, Mumbai, India; CKU, Chen Kung University, Tainan, Taiwan; LACM, Los Angeles County Museum of Natural History, Los Angeles, CA; MNHN, Muséum national d'Histoire naturelle, Paris; NJNU, Nanjing Normal University, Nanjing, China; NSMT, National Science Museum, Tokyo; NMNS, National Museum of Natural Science, Taichung, Taiwan; ONHM, Oman Natural History Museum, Muscat; OPCF, Ocean Park Conservation Foundation, Hong Kong; OW, Ocean World, Yehliu, Taiwan; PEM, Port Elizabeth Museum, South Africa; QM, Queensland Museum, Brisbane, Australia; RSLM, R. S. Lal Mohan personal collection, Nagercoil, India; SAM, South Australian Museum, Adelaide, Australia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SWFSC, Southwest Fisheries Science Center (Marine Mammal Synoptic Collection), La Jolla, CA; USNM, National Museum of Natural History, Washington, DC; WT CB, Cua Be Whale Temple, Nha Trang, Vietnam; WT VL, Vinh Loung Whale Temple, Nha Trang, Vietnam; WT VT, Vung Tau Whale Temple, Vung Tau, Vietnam; ZAM, South African Museum, Capetown, South Africa; ZMA, Zoological Museum, University of Amsterdam, the Netherlands.

APPENDIX III

REVIEW OF NOMINAL SPECIES POTENTIALLY RELATED TO *D. CAPENSIS TROPICALIS*

Delphinus longirostris G. Cuvier, 1829

The species is based on a specimen collected from the Malabar coast of India by J. J. Dussumier in 1827, which is stored in the Muséum national d'Histoire naturelle (Paris Museum, MNHN A-3065). We measured the specimen for this study. Cuvier (1829) described this new species of dolphin as *Delphinus longirostris*. This name is unavailable, as it is preoccupied by *Delphinus longirostris* Gray, 1828, which is now in the synonymy of *Stenella longirostris* (the pantropical spinner dolphin; see Perrin 1998).

Delphinus sao Gray, 1846

The type locality for *Delphinus sao* is Madagascar, which is potentially in the range of the Indo-Pacific common dolphin (however, based on what we currently know of *Delphinus*, it would more likely be a specimen of *D. capensis capensis*). Gray (1846) stated that the type was located in the Paris Museum, and in fact there are currently two skulls in the Paris Museum (MNHN A 3037 and MNHN 1928-162) that could correspond to the type.[12] We examined both skulls, and found both of them to be examples of *Stenella attenuata* (the pantropical spotted dolphin), and tooth counts of neither skull match those reported for the type of *D. sao*. Due to these uncertainties, D. Robineau (footnote 11) has suggested, therefore, that *D. sao* Gray, 1846 be considered a *nomen dubium* (ICZN 1999), and we concur.

Delphinus frithii Blyth, 1859

The exact type locality is not known, but since the type specimen was collected during a voyage from the United Kingdom to India, it may be from within the range of the

[12] Personal communication from D. Robineau, Muséum national d'Histoire naturelle, 55 Rue Buffon, Paris 75005, France, September 1999.

Indo-Pacific common dolphin. Heyning and Perrin (1994) associated it with the long-beaked common dolphin (*D. capensis*), based on published tooth counts of 55/50. The type was reported to be in the Calcutta Museum by Sclater (1981). However, during a visit to Calcutta by the senior author in April 2000, the skull could be found in neither the collection of the Indian Museum (the new name for the Calcutta Museum), nor that of the Zoological Survey of India (where many of the specimens from the old Indian Museum are now housed). Due to the uncertain status of this type, we suggest that *Delphinus frithii* Blyth, 1859 be considered a *nomen dubium* (ICZN 1999).

Delphinus pomeegra Owen, 1866

The type skull was supposedly collected from the coast of India (Madras), and is in the collection of the Natural History Museum, London (BM 1866.2.5.5). The senior author examined and measured the type skull in 1999. Although it is presumably an example of the Indo-Pacific common dolphin, the specimen was immature (CBL = *ca.* 405 mm) and the skull is badly damaged, thereby making it a *nomen dubium* (Heyning and Perrin 1994).

Delphinus dussumieri Blanford, 1888

This is a new name proposed by Blanford (1888) for *D. longirostris* G. Cuvier, 1829. However, this name is also unavailable, as it is preoccupied by *D. dussumieri* Fischer, 1829, which is a considered to be a junior synonym of *Cephalorhynchus heavisidii* (Haviside's dolphin; Hershkovitz 1966).

Delphinus tropicalis van Bree, 1971

This new name was proposed by van Bree (1971*a*) for the Indo-Pacific common dolphin, upon realization that both *D. longirostris* G. Cuvier, 1829 and *D. dussumieri* Blanford, 1888 were preoccupied. This name has been used since 1971 to refer to the Indo-Pacific common dolphin by most authors who considered it to be a valid species (*e.g.*, Pilleri and Gihr 1972*a*, *b*).

Conclusion

The appropriate name to be used for the Indo-Pacific common dolphin is *Delphinus capensis tropicalis* (van Bree, 1971). We suggest that the nominate subspecies of the long-beaked common dolphin should be referred to as *Delphinus capensis capensis* Gray, 1828.

Appendix IV

Review of Additional Information on *Delphinus capensis tropicalis* (van Bree, 1971)

Because there is not much known about Indo-Pacific common dolphins, and much of what is known is scattered in difficult-to-find literature, we present a review of information on the biology of these animals not covered in the above subspecies description.

Anatomy, Life History, and Ecology

There has been very little study of the anatomy and physiology of *tropicalis*-form common dolphins, although Pilleri and Gihr (1972*a*) provided general descriptions of the

brain, heart, spleen, pseudopancreas, kidneys, and testes. The optic and cochlear nerves of a Chinese specimen were described by Gao and Zhou (1991, 1992).

The majority of information on the biology of the *tropicalis*-form common dolphin comes from stranded and incidentally killed specimens. There have been no detailed studies of the ecology of this form, and information on life history is scarce. A 220-cm specimen from southern China weighed 102 kg (Zhou *et al.* 1980), and Wang (1990) reported a maximum weight of 110 kg for a 181-cm specimen from China.

Females dominated the sex ratio (1:1.8) of animals taken in nets off Calicut, India (Lal Mohan 1985*b*). There is little evidence of seasonality in calving. Calves have been observed in March off Somalia (Small and Small 1991), January in the Red Sea (Alling 1986), and January, April, May, November, and December around the Arabian Peninsula.[13] Lal Mohan (1995) reported a specimen of 167 cm length with one growth layer group (GLG) and another of 170 cm with four GLGs. He suggested that sexual maturity probably occurs at around 200 cm. The testes of a 256-cm adult male weighed 1,835 g (left) and 1,775 g (right) (Pilleri and Gihr 1972*a*).

Squid remains and fish have been found in stomachs of *tropicalis*-form common dolphins (Pilleri and Gihr 1972*a*). The stomach of one specimen from Calicut, India, contained 10 mackerels (James *et al.* 1987). These dolphins have been seen in association with *Sardinella* sp., various tunas, and several other organisms off Somalia (Small and Small 1991).

There are few records of parasites in this subspecies. In one specimen from Pakistan, Pilleri and Gihr (1972*a*) found stomach nematodes, later identified as *Anisakis typica* (Pilleri 1974). Cirriped barnacles have been found attached to the teeth and gums (Pilleri and Gihr 1972*a*). Hamsa and Nammalwar (1978) reported the isopod *Cirolana parva* from the eyeballs of a common dolphin from India, but the species identification of the dolphin is open to question.

Behavior

Because of the paucity of documented at-sea sightings of this form of common dolphin, knowledge of the behavior of these animals is poor. These dolphins often ride the bow waves of vessels (Baldwin and Salm 1994, Robineau and Fiquet 1996, Smeenk *et al.* 1996, Ballance and Pitman 1998), but Alling (1986) reported that most groups she observed in the northern Indian Ocean did not bowride. This may be a result of having been hunted there. Some possible evidence of seasonal movements was noted by Lal Mohan (1985*b*) for India, in which 57% of the specimens were landed in September to November.

There is great variability in group size, with schools in offshore areas somewhat larger than coastal ones. Reported group sizes are 3–200 off Somalia (Small and Small 1991), 15–1,700 (with an average of 221) off Oman (Ballance and Pitman 1998), 2–12 in the Persian Gulf (Henningsen and Constantine 1992), 2–60 off Saudi Arabia (Robineau and Fiquet 1996), 2–100 in the Red Sea (Smeenk *et al.* 1996, Baldwin *et al.* 1998), 3–200 (most between 20 and 50) in the northern Indian Ocean (Alling 1986), and 15–35 in the Strait of Malacca and Andaman Sea (Leatherwood *et al.* 1984). Off Oman, they often form mixed schools with spinner dolphins (*Stenella longirostris*), generally remaining on the outskirts of the spinner school (Baldwin and Salm 1994, Ballance and Pitman 1998, Van Waerebeek *et al.* 1999). Associations with unidentified *Stenella* spp. have also been noted for the Red Sea (Smeenk *et al.* 1996).

[13] Baldwin, R., K. Van Waerebeek and M. Gallagher. 1998. A review of small cetaceans from waters off the Arabian Peninsula. International Whaling Commission Scientific Committee Report SC/50/SM6 (unpublished). Available from the International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge CB4 9NP, U.K.

Conservation Status

Common dolphins of the *tropicalis*-form do not appear to be particularly rare within their range. In particular, there are many records from the Arabian Peninsula area, and they are well known in the Persian Gulf and northern Arabian Sea. Robineau and Fiquet (1996) found them to be the most commonly sighted small cetaceans around Abu Ali Island, Saudi Arabia, and Baldwin *et al.* (1998) considered them to be the most common cetacean in Oman. They are not as commonly taken as dolphins of the genus *Stenella* off Sri Lanka (Leatherwood and Reeves 1989, Ilangakoon 1997), and in the eastern part of their range in southeast Asia, other species of offshore small cetaceans (such as *Stenella attenuata* and *S. longirostris*) appear to be much more common.

In several parts of the range, there is evidence of incidental takes in fisheries. Gallagher (1991) found one dolphin apparently butchered near a fishing vessel in the United Arab Emirates, and another specimen was found on the beach with the back muscles filleted. One was taken in a surface gillnet off Somalia (Small and Small 1991). Five dolphins with clear gillnet markings on the body were found in Omani waters (Salm *et al.* 1993). They are probably taken in fishing nets in other parts of the Arabian Gulf area as well (Baldwin *et al.* 1998).

In India, dolphins are caught and killed in gillnets off at least Bombay, Goa, Malangore, Calicut, Cochin, Mandapam, and Quilon (James and Lal Mohan 1987, Mahadevan Pillai and Chandrangathan 1990, Lal Mohan 1994, Jayaprakesh *et al.* 1995). They are also at least occasionally taken in trawl nets and purse seines in India (Jayaprakesh *et al.* 1995, Krishna Pillai and Lipton 1996). In some parts of India, such as Cochin, Nagercoil, and Quilon, captured common dolphins are brought ashore by fishermen for sale at local fish markets, sometimes still alive (James *et al.* 1987, Mahadevan Pillai and Chandrangathan 1990, Jayaprakesh *et al.* 1995). The fact that there is apparently a market for selling the flesh indicates the potential for some directed killing of common dolphins along the coast of India.

This is one of many species known to be killed in gillnets off Sri Lanka (Leatherwood and Reeves 1989). Ilangakoon (1997) documented two specimens taken either by gillnet or by harpoon in Sri Lanka—this also indicates the possibility of direct takes there. A common dolphin was reported to be caught in a tuna longline at the Andaman Islands (Sivaprakasam 1980), but the species identification is in question (see footnote 9). Common dolphins, possibly of this subspecies, are frequently taken in fishing operations along the coast of China (Wang 1984, 1985, 1990).

Dolphins have historically been killed directly in Oman and this practice still continues today (Baldwin *et al.* 1998, Salm *et al.* 1993). Some of the catches known for India and Sri Lanka may have been deliberate (see above). Additional threats that have been identified are poisoning by red tides, boat traffic, pollution, and general habitat loss and degradation (Baldwin *et al.* 1998).