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Cranial variation in common dolphins *Delphinus* spp. off South Africa, with the inclusion of information from the holotype of *Delphinus capensis*

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The common dolphins (genus *Delphinus*) are widely distributed in all temperate and tropical oceans. Over this wide geographical distribution they show considerable range in morphological variation, which has led to descriptions of several species in the genus. Until recently, only two species of *Delphinus* were accepted, but this classification has become contentious. This study investigated the occurrence of morphologically different types of *Delphinus* in South African waters and assessed geographic and morphometric variations within each type. A total of 296 skulls of *Delphinus* spp., obtained from the Port Elizabeth Museum and the Iziko South African Museum, were photographed in their dorsal and ventral aspects for geometric morphometric analysis. Our results revealed three clusters of specimens based on analysis of the dorsal aspect of the skull, and two clusters for the ventral aspect. Significant differences in cranial size were found between clusters. Both cranial aspects showed that the main variations in skull shape occurred in the rostral region and braincase area, indicating divergent adaptations relating to these features. There was a substantial difference between the composition of the dorsal-aspect and ventral-aspect clusters, suggesting the presence of only one species in South African waters. Significant differences between morphological clusters associated with the three regions within the study area (cold-temperate, warm-temperate and subtropical) are probably mediated through differences in local environmental conditions (e.g. different water temperatures and productivity).

Keywords: cranial morphology, *Delphinus delphis*, geographical variation, geometric morphometrics, rostral index, sexual dimorphism, taxonomy

Introduction

Morphology plays an important role in the ecology and life history of all animals, including cetaceans (Perrin 1975; Heyning and Lento 2002; Galatius 2010). Historically, morphological information presented the primary data utilised by taxonomists to investigate the status of species and subspecies (Robineau et al. 2007; Zinetti et al. 2013). Analysis of morphology has been used frequently, together with molecular analysis, to clarify the taxonomic status of a variety of animals (Galatius and Gol'din 2011; Jacquet et al. 2013; Mendez et al. 2013; Jefferson and Rosenbaum 2014). Due to the availability of crania and their morphological complexity, examining skull morphology is the most frequently used technique to study differences between and within populations of cetaceans (Ross 1977; Jefferson 2002; Kemper 2004).

Common dolphins *Delphinus* spp. are widely distributed throughout temperate and subtropical oceans (Neumann et al. 2002; Murphy and Rogan 2006). Perhaps owing to their wide geographical distribution, they show considerable morphological variation over their reported ranges and this has led to the description of several species over the years (Natoli et al. 2006). With more than 20 species of *Delphinus* described,

population assessments became complicated and the taxonomic status controversial (Watson 1981; Natoli et al. 2006). Heyning and Perrin (1994) synonymised the majority of these species, suggesting two species only, *D. delphis* Linnaeus, 1758 and *D. capensis* Gray, 1828. This re-description was based on animals found off the North Pacific coast of the United States, and was carried out using morphological characteristics (Heyning and Perrin 1994). Thereafter, two species of *Delphinus* were recognised: the short-beaked common dolphin (*D. delphis*) and the long-beaked common dolphin (*D. capensis*) (Heyning and Perrin 1994). *Delphinus delphis* was thought to be widely distributed, mostly in the temperate and tropical Atlantic and Pacific oceans, and in the southwestern extreme of the Indian Ocean (Jefferson et al. 2008, 2009). *Delphinus capensis* was believed to have a more disjunct and restricted range, being distributed in the Indian Ocean from the South African coast to Southeast Asia, southern Japan, along the Californian, Mexican and Peruvian coasts and in the Atlantic along the west coast of Africa south of Angola, and along the coast of South America between Venezuela and Argentina (Hammond et al. 2008).

The validity of the two species has generally been supported over the past few decades, but there have been uncertainties about the taxonomy of the common dolphins within their proposed respective ranges (Perrin et al. 2013). Investigations of variation in cranial and external morphology have revealed gaps in our understanding of the taxonomy of these dolphins (Murphy et al. 2006). Genetic studies have also suggested uncertainty regarding taxonomic and phylogenetic relationships within this genus, and have particularly cast doubt on the status of *D. capensis* (Amaral et al. 2012a, 2012b; Murphy et al. 2013). Recently, Cunha et al. (2015) suggested the invalidity of *D. capensis* based on molecular data, which included sequences for the long-beaked (*D. capensis*) morphotype from the west coast of South Africa. The Committee on Taxonomy (2018) of the Society for Marine Mammalogy has followed Cunha et al.'s (2015) recommendations, although animals found along the south and east coasts of South Africa were not included in that analysis. Thus, only one species, *D. delphis*, is currently accepted in this genus. In light of this uncertainty, further work, particularly involving the holotype of *D. capensis*, is necessary to elucidate the taxonomy of *Delphinus* species on a global scale.

As elsewhere, the distribution and composition of *Delphinus* spp. in South African waters is also subject to debate. Publications on *Delphinus* in South African waters prior to the taxonomic revision of Heyning and Perrin (1994) refer to all specimens as *D. delphis* (Best 2007). However, since Heyning and Perrin's (1994) study, the majority of specimens from the South African coast have been ascribed to *D. capensis* (Jefferson and Van Waerebeek 2002; Samaai et al. 2005; Natoli et al. 2006). In studies based on the cranial morphometrics of 153 (Jefferson and Van Waerebeek 2002) and 72 (Samaai et al. 2005) common dolphin skulls from South Africa, it was concluded that almost all common dolphin specimens from South Africa were *D. capensis*. The exceptions were three specimens with *D. delphis* characteristics that were described by Samaai et al. (2005), which suggested the possibility of the latter species occurring off the west coast of South Africa. In addition, Samaai et al. (2005) suggested that parasite and stomach-content data showed that *D. capensis* off South Africa had a more inshore distribution than *D. delphis*. Furthermore, Natoli et al. (2006) reported that molecular analysis indicated that South African common dolphins showed the highest differentiation when compared with other populations in the world. None of these previous studies have included large numbers of specimens from the entire South African coastline, or the cranial morphological characteristics of the *D. capensis* holotype.

This study aimed primarily to clarify the taxonomic status of *Delphinus* spp. inhabiting South African waters, by using cranial morphology, including new data on the holotype of *D. capensis*. In addition, we examined geographic variation within the genus and between potential taxonomic units detected in the analyses.

Methods

Collection of data

Crania of *Delphinus* specimens were obtained from the Graham Ross Marine Mammal collection at the Port

Elizabeth Museum and the Iziko South African Museum. These specimens originate from various sources, including bycatch in shark nets off the coast of KwaZulu-Natal (some 80% of specimens) and dolphins stranded between St Helena Bay on the west coast and the Mozambique border on the east coast (Figure 1). The specimens were grouped according to geographic regions defined by Branch and Branch (1981), namely the cold-temperate region (St Helena Bay – Cape Agulhas), warm-temperate region (Cape Agulhas – near Mzamba), and subtropical region (near Mzamba – Mozambique border) (Figure 1).

A total of 296 adult crania of *Delphinus* spp., from three regions (i.e. cold-temperate [CT], $n = 28$; warm-temperate [WT], $n = 54$; and subtropical [ST], $n = 214$), as well as the holotype of *D. capensis* from the Natural History Museum, London (BM 41.1734), were photographed and used for analysis of cranial morphology. Physical maturity was determined using the degree of fusion between the maxillae and premaxillae, with mature individuals determined as having at least 50% of the length of the dorsal aspect of the rostrum fused (Perrin and Heyning 1993). Before each specimen was photographed, a spirit level was used to achieve a standard orientation, set up to minimise the vertical distance between landmarks. Photographs were taken using a Panasonic Lumix DMC-FZ50 digital camera with the lens set at 35 mm. A dark background was used to emphasise outlines (i.e. maximise contrast), and a tripod and an extension were used to position the camera lens at an arbitrarily chosen standard height of 76 cm. A 30-cm ruler was placed at an elevated level alongside each skull to provide a measure of scale at a plane close to that of the landmarks.

The resulting JPG images were then cropped and converted into TPS files using the program tpsUtil and imported into the mathematical software tpsDig 2.05 (Rohlf 2006). A set of dorsal (16) and ventral (19) landmarks were digitised onto the photograph of each skull (Rohlf 2006) for analysis (Figure 2). Descriptions of the positions of the landmarks are given in Table 1.

Data analysis

Prior to all analyses, the raw coordinates were transformed into Procrustes coordinates of landmarks to eliminate variation related to position, size and rotation, using the program MorphoJ (Klingenberg 2011). Data were corrected for allometric variation by performing further shape analyses on the residuals of a multivariate linear regression of shape (Procrustes coordinates) on centroid size (CS), where CS is defined as the square root of the summed squared distances from each landmark to the centroid of the configuration (Zelditch et al. 2004). A simple linear regression was chosen over a regression on log CS, because the amounts of explained variance of regressions were almost identical when using CS and log CS as dependent variables. The program PAST (Hammer et al. 2001) was used to construct phenetic clusters to assign specimens to groups and assess size variation, while MorphoJ was used for shape variation analyses. Defined clusters were thereafter treated as separate entities. A linear discriminant analysis was used to further analyse the shape differences between major clusters detected, to

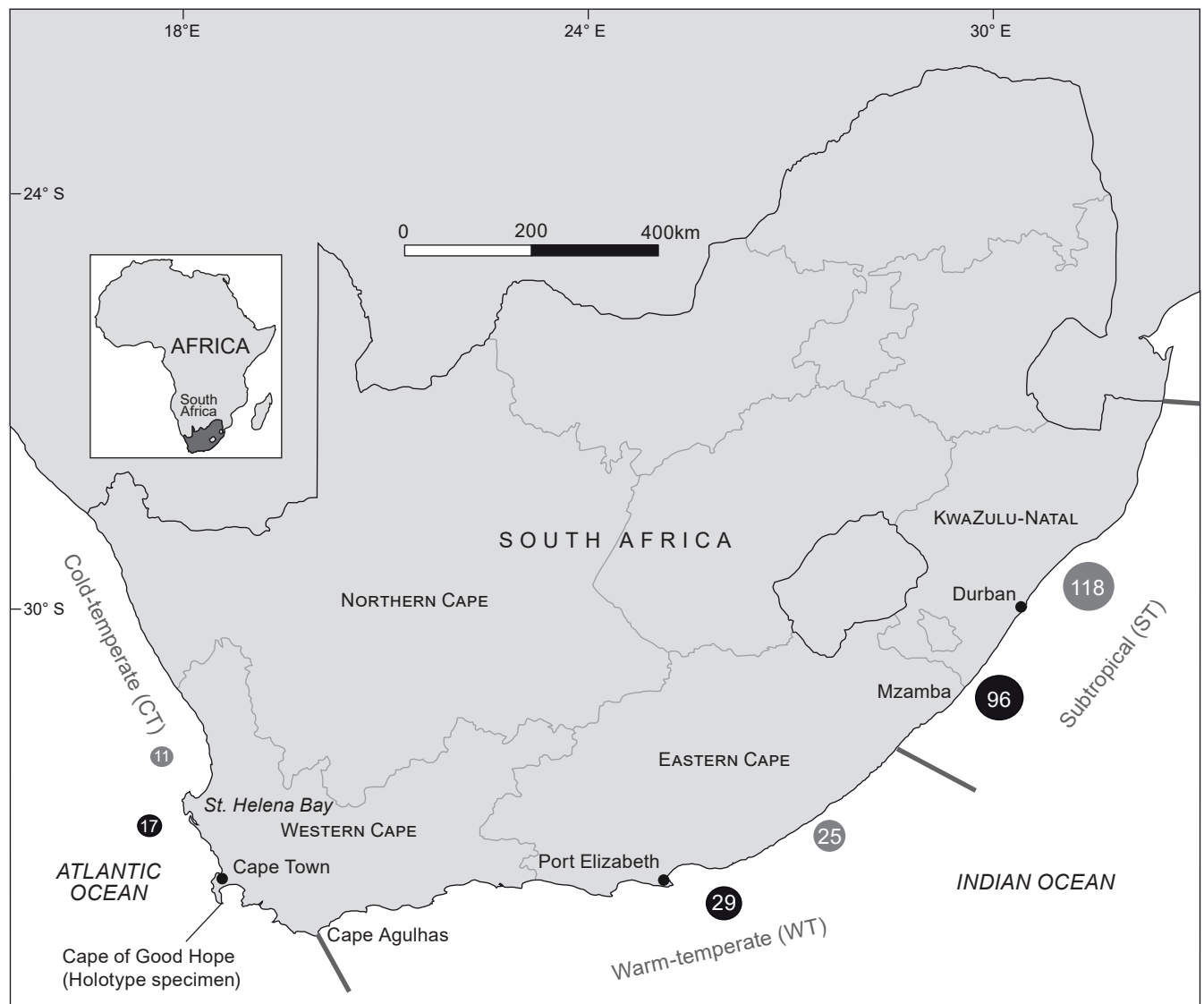


Figure 1: Map showing the numbers of crania of *Delphinus* specimens, specified by sex (males, black circles; females, grey circles), from the three geographic regions of South Africa as defined by Branch and Branch (1981)

assess differences and examine how well these clusters could be separated based on skull shape. Centroid size (CS) was used to investigate differences in size. These size data were tested for normality using the Shapiro–Wilk test. Two-way analysis of variance (ANOVA; Pares-Casanova and Fabre 2013) was used to compare size between sexes and between regions. Discriminant function analysis (DFA) using jackknife/leave-one-out cross-validation was used to investigate: (i) shape differences between groups; (ii) sexual dimorphism of shape in the whole sample; (iii) sexual dimorphism within regions; and (iv) shape differences between regions. Permutation tests (1 000 repetitions) were used to assess the significance of Procrustes and Mahalanobis distances between groups. Overlap in the distribution of the dorsal-aspect and ventral-aspect clusters was assessed using the G-test of goodness-of-fit (Sokal and Rohlf 1969). Lastly, crania were measured to calculate the rostral index, which is the ratio of

the rostrum length to the zygomatic width. Previous studies have used this as a diagnostic feature in determining species for *Delphinus* (Heyning and Perrin 1994; Tavares et al. 2010).

Results

Cluster analysis and cranial size variation

Cluster analysis using the unweighted pair group method with arithmetic mean of the dorsal aspect revealed three major clusters, with Cluster D1 (Dorsal 1) comprising 10 specimens of both females and males, 8 of which were from the subtropical region (Appendix; Figure 3). Cluster D2 (Dorsal 2) comprised 218 specimens (including the *D. capensis* holotype), with all regions well represented (Appendix; Figure 3). Cluster D3 (Dorsal 3) comprised 54 specimens, with all regions represented (Appendix; Figure 3). In contrast, only two clusters were identified for

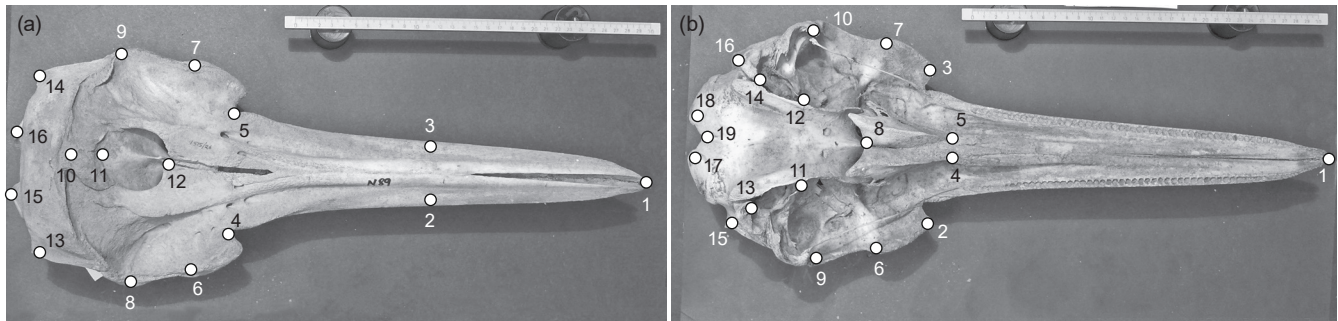


Figure 2: The landmarks digitised on the dorsal (left) and ventral (right) aspects of the cranium for each *Delphinus* specimen

Table 1: Description of landmarks used for the analysis of phenology, size and shape, for both the dorsal and ventral aspects of each *Delphinus* cranium

Landmark number	Description
<i>Dorsal cranial view</i>	
1	Rostral tip
2 and 3	Midpoint between the anteriormost point of antorbital notch and rostral tip/midpoint of the rostrum; right and left
4 and 5	Antorbital notch, right and left
6 and 7	Intersection between the frontal bone and the zygomatic process, right and left
8 and 9	Intersection between the parietal bone and the frontal interparietal suture, right and left
10	Anteriormost point of the nuchal crest
11	Midpoint of the nasal bone suture
12	Posteriormost point in the premaxilla bone
13 and 14	Posteriormost point on the curve of the parietal bone, right and left
15 and 16	Posteriormost point on the occipital condyle, right and left
<i>Ventral cranial view</i>	
1	Rostral tip
2 and 3	Anteriormost point on the antorbital notch in the maxilla, left and right
4 and 5	Anteriormost point of the palatine surface of the pterygoid, left and right
6 and 7	Intersection between the frontal bone and the zygomatic process, left and right
8	Anteriormost point between the two pterygoid hamuli
9 and 10	Intersection between the parietal bone and the frontal interparietal suture, left and right
11 and 12	Externalmost point of the suture between the basioccipital crest and the pharyngeal crest (choanae), left and right
13 and 14	Posteriormost point on the paraoccipital process curve of the parietal bone, left and right
15 and 16	Posteriormost point on the curve of the occipital bone, left and right
17 and 18	Posteriormost point on the edge of the supraoccipital bone, left and right
19	Midpoint of the intercondyloid notch

the ventral aspect, after removing outliers, with Cluster V1 (Ventral 1) comprising 18 specimens, and Cluster V2 (Ventral 2) comprising all the remaining specimens ($n = 242$) in the sample (Appendix; Figure 4). Cluster V2 contained specimens mainly from the warm-temperate and the subtropical regions, together with one male specimen from the cold-temperate region (Appendix; Figure 4). The distribution of crania between the clusters was significantly different between the dorsal and ventral aspects ($GG = 11.947$, $df = 1$, $p < 0.01$).

Significant differences in CS for the dorsal aspect were observed among the three clusters ($F = 25.72$, $p < 0.001$) and between sexes ($F = 141.8$, $p < 0.001$). For the ventral aspect, significant differences were also observed between the two clusters ($F = 4.26$, $p < 0.05$) and between sexes ($F = 22.65$, $p < 0.001$). Furthermore, Clusters V2 and D2 showed larger variations within the sample, which could be due to the relatively large sizes of these groups (Appendix).

Variation in ventral shape assessed by discriminant function analysis (DFA)

Based on the dorsal aspect, there were significant differences in relation to shape between the three clusters (Mahalanobis distance 1–2; 1–3; 2–3 = 2.990; 5.593; 2.688; $p < 0.001$) and the sexes (Mahalanobis distance = 0.803; $p < 0.001$) (Table 2). Significant differences were also detected with regard to shape between clusters for the ventral aspect (Mahalanobis distance = 2.66; $p < 0.001$) and the sexes (Mahalanobis distance = 0.740; $p < 0.01$) (Table 2). To test for reliability of the DFA, leave-one-out cross-validation classification was used (Table 2). The visual representations of the thin-plate spline deformation grids and wireframe graphs showed that, dorsally, the main shape-changes of the cranium along canonical variate 1 (CV1) occurred in: (i) rostral length and width; (ii) the antorbital notches; (iii) the intersections between frontal bones and the zygomatic processes; (iv) the parietal bones

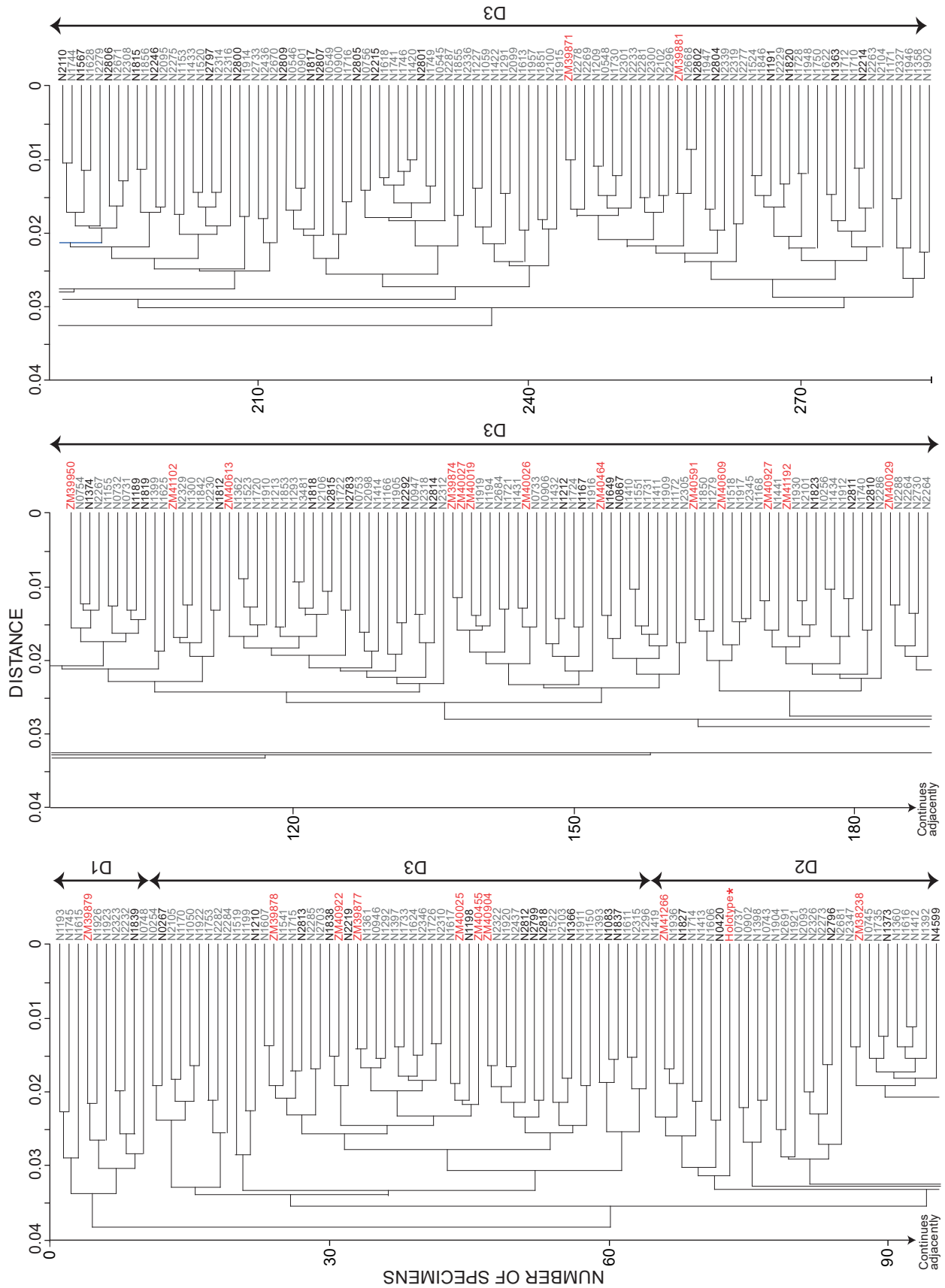


Figure 3: UPGMA phenogram computed on the matrix of Procrustes distances among mean dorsal features in the cranial shape of both female and male *Delphinus* from South Africa. D1, D2, and D3 are putative major clusters. Cluster D1: black; Cluster V2: grey. The red asterisk denotes the holotype of *Delphinus capensis*

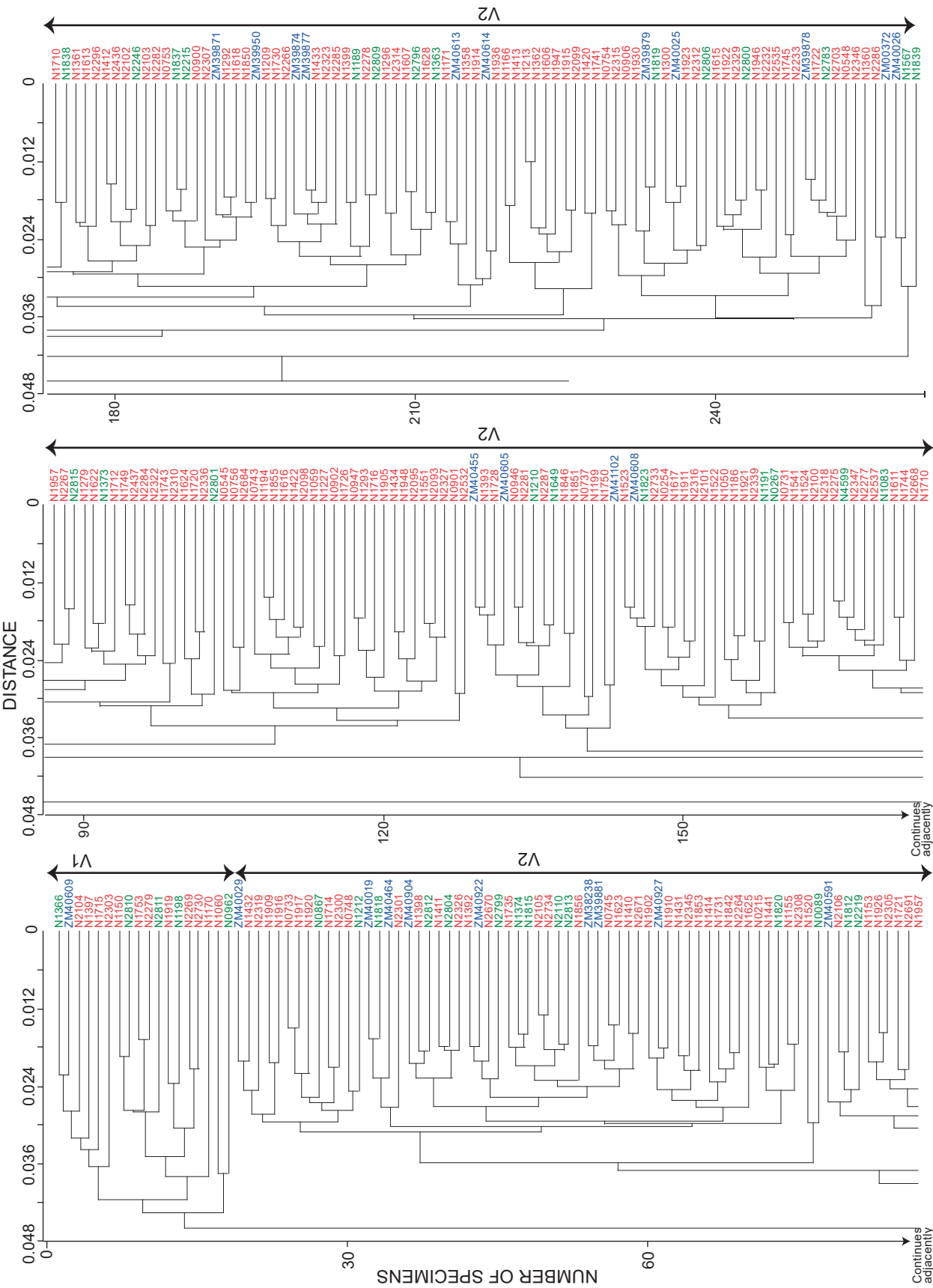


Figure 4: UPGMA phenogram computed on the matrix of Procrustes distances among mean ventral features in the cranial shape of female and male *Delphinus* from South Africa. V1 and V2 are putative major clusters. Colours denote specimens from different regions: blue = cold-temperate; green = warm-temperate; red = subtropical

Table 2: (a) The discriminant function analysis pairwise Mahalanobis and Procrustes distances, and (b) leave-one-out cross-validation classification, between clusters and sexes for dorsal and ventral aspects of the crania of *Delphinus*. Significant *p*-values from the permutation tests are indicated by an asterisk. $\alpha = 0.01$

(a) Discriminant function analysis		
Groups	Mahalanobis distance	Procrustes distance
<i>Dorsal aspect</i>		
1–2	2.99*	0.02*
1–3	5.60*	0.04*
2–3	2.69*	0.02*
Females–Males	0.80*	0.01*
<i>Ventral aspect</i>		
1–2	2.66*	0.03*
Females–Males	0.74*	0.01*

(b) Leave-one-out cross-validation classification				
<i>Dorsal aspect</i>				
True group	Group allocated to			
	Cluster 1	Cluster 2	Total	% Correct
Cluster 1	8	2	10	80
Cluster 2	19	199	218	91
<i>Dorsal aspect</i>				
	Cluster 1	Cluster 3	Total	% Correct
Cluster 1	10	0	10	100
Cluster 3	1	53	54	98
<i>Dorsal aspect</i>				
	Cluster 2	Cluster 3	Total	% Correct
Cluster 2	198	20	218	76
Cluster 3	5	49	54	79
<i>Dorsal aspect</i>				
	Females	Males	Total	% Correct
Females	83	63	146	56
Males	56	80	136	58
<i>Ventral aspect</i>				
	Cluster 1	Cluster 2	Total	% Correct
Cluster 1	13	5	18	72
Cluster 2	24	218	242	90
<i>Ventral aspect</i>				
	Females	Males	Total	% Correct
Females	76	56	132	57.6
Males	58	70	128	55

and the frontal interparietal sutures; (v) the posterior point on the curve of the parietal bones; and (vi) the occipital condyles (Figure 5).

For the ventral aspect, differences between the two clusters were in: (i) rostral width and length; (ii) the anteriormost points on the antorbital notches of the maxillae; (iii) the palatine surface of the pterygoids; (iv) intersections between the frontal bones and zygomatic processes; (v) the parietal bones and the frontal interparietal suture; (vi) posteriormost points on the paraoccipital process curve of the parietal bone; and (vii) the edge of the supraoccipital bones (Figure 5). This clearly showed that the main differences between the two clusters for the ventral aspect were in the rostral area, the braincase region, and the posteriormost region of the cranium. This meant that most of the Cluster-V2 specimens were characterised by longer, narrower rostra and rounder braincases (Figure 5). In contrast, Cluster-V1 specimens were characterised by shorter but wider rostra, broadened braincases, and wider palatine surfaces in the ventral aspect as compared with Cluster-V2 specimens (Figure 5).

Rostral index

The frequency of the rostral index followed a normal

distribution; hence, there was no discrete separation representing two species in the data (Figure 6). Only eight individuals had a rostral index below 1.52, which placed them within the range of the short-beaked common dolphin (Heyning and Perrin 1994) (Figure 6). The great majority of individuals, including the holotype (1.75), had a rostral index between 1.52 and 1.79, which is within the range of the long-beaked common dolphin (Figure 6).

Variation in cranial size within clusters

As a result of insufficient data, tests for differences in cranial size between sexes and geographical regions could not be carried out for Cluster D1 (Appendix). Clusters D2 and D3 showed significant within-cluster sexual dimorphism ($F_{D2} = 145.80$, $p < 0.001$; $F_{D3} = 19.48$, $p < 0.001$). Cluster D2 also showed significant differences between regions ($F = 11.07$, $p < 0.001$), whereas no significant differences were found between regions in Cluster D3 ($F = 0.535$, $p = 0.589$). In both clusters (D2 and D3), males had larger average centroid sizes than females (Appendix). There were size differences between the regions in Cluster D2, wherein the cold-temperate specimens were larger than the subtropical and

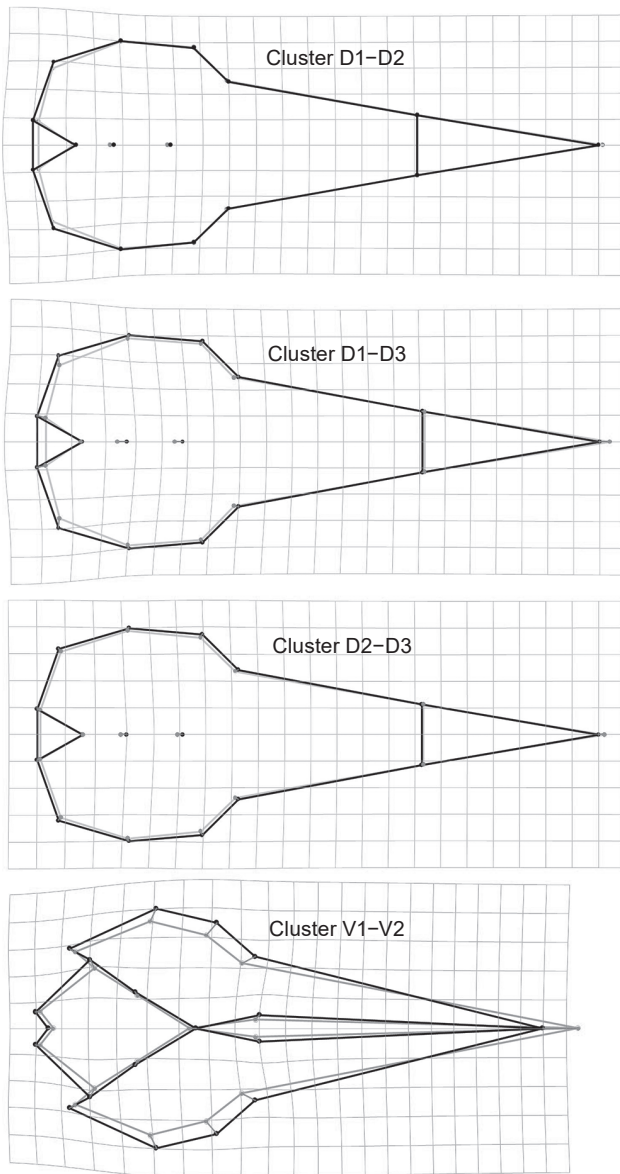


Figure 5: Visualisation of shape differences associated with discriminant vectors between specimens in the dorsal and ventral aspects of the crania of *Delphinus* spp. from South Africa

warm-temperate specimens (Appendix).

In the analysis of the ventral aspect, the cold-temperate region was not included in statistical tests because only one specimen was available (Appendix). With regard to size in Cluster V1, neither sexual dimorphism ($F = 1.32$, $p = 0.437$) nor interregional differences were significant ($F = 0.299$, $p = 0.593$). However, in Cluster V2, sexual dimorphism was significant ($F = 26.4$, $p < 0.001$). Between regions, the two-way ANOVA revealed significant differences for the ventral aspect ($F = 6.45$, $p = 0.002$).

Size differences between sexes in both aspects revealed that males had a larger average centroid size as compared with females (Appendix). There were differences between the regions in both aspects, wherein the cold-temperate specimens had larger crania as compared with the

subtropical and warm-temperate specimens (Appendix).

Cranial-shape variation within clusters

With one exception, no significant differences were detected in cranial shape between sexes or regions within any cluster for either the dorsal or ventral aspect (Table 3). Due to the smaller sample size, DFA could not be performed between some regions, such as CT–WT. The sole exception was for Cluster D2, where the DFA revealed a significant shape difference between sexes (Table 3).

Discussion

Taxonomy

It has been suggested that taxonomic clarification of *Delphinus* spp. using specimens from South African waters could importantly assist our understanding of the global taxonomy of this genus (Kemper 2004). Local taxonomic studies are also important as they allow management of unique units and marine spatial protection.

When using cranial features to differentiate between *Delphinus* taxa, a commonly used feature is the ratio of the rostral length to the zygomatic width (Heyning and Perrin 1994; Bell et al. 2002; Samaai et al. 2005; Tavares et al. 2010). For example, for specimens of *D. delphis* from the North Pacific, this ratio falls within the range 1.21–1.47, whereas specimens assigned to *D. capensis* have shown ratios of 1.52–1.77 (Heyning and Perrin 1994). In contrast, the ratio for the subspecies *D. c. tropicalis* ranges from 1.60 to 2.06 (Jefferson and Van Waerebeek 2002). Heyning and Perrin (1994) described the skull of *D. capensis* from the North Pacific as being larger and narrower, with a longer rostral length, as compared with the skull of *D. delphis* from the same region. In the present study there were few individuals that had a ratio between 1.47 and 1.52. Instead, the rostral index of the specimens ranged between 1.52 and 1.79, which is within the ranges reported for *D. capensis* and the subspecies *D. c. tropicalis*.

In this study, specimens of Cluster V1 were characterised by shorter and broader rostra, their braincases were broader and they had a wider palatine surface of the pterygoids as compared with the specimens of Cluster V2. It was also found that the specimens of Cluster V1 were significantly smaller than those of Cluster V2. The specimens in Cluster D3 were characterised by longer, narrower rostra, a more-rounded cranium, and a narrower palatine surface of the pterygoids as compared with specimens of Cluster D1. Cluster-D2 specimens were intermediate, falling between the specimens in Clusters D1 and D3.

According to published descriptions of cranial morphology, Clusters D2 and D3 could be *D. capensis* as they shared characters of that species, such as the narrower, longer rostra and smaller braincases, whereas Cluster D1 shared the characteristics of *D. delphis*, with wider, shorter rostra and slightly wider braincases. Notably, the *D. capensis* holotype was situated in Cluster D2. In terms of the ventral aspect, Cluster-V1 specimens could be *D. delphis*, whereas Cluster-V2 specimens could be *D. capensis*. Interestingly, the distribution of specimens in clusters for the dorsal aspect did not reflect their distribution in the cluster for the ventral aspect. A goodness-of-fit test indicated that specimens from a particular group of one aspect were

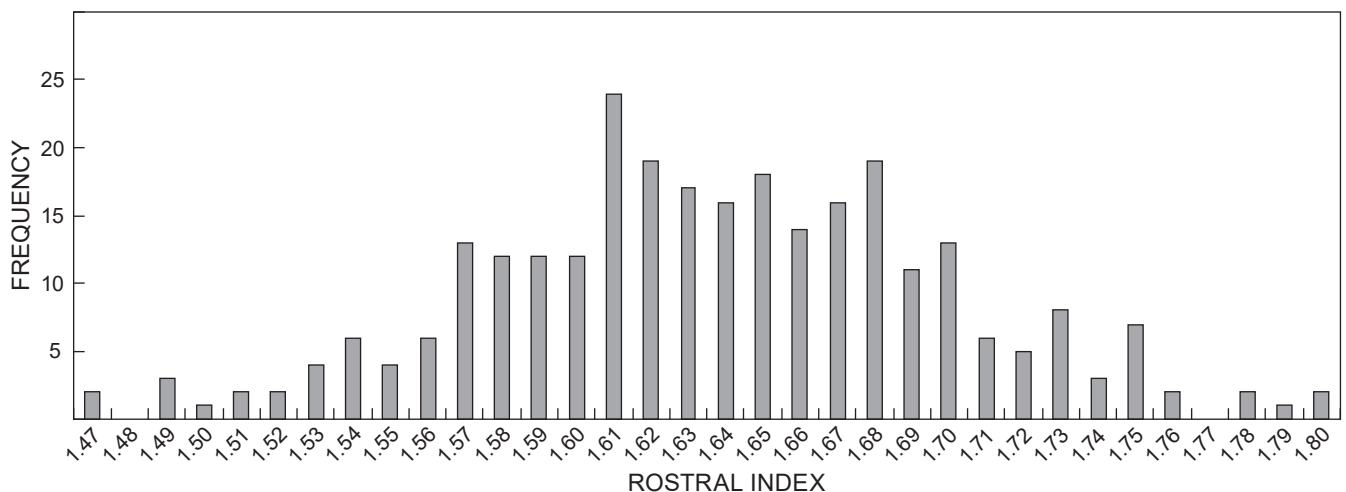


Figure 6: Frequency distribution of the rostral index of *Delphinus* specimens measured in this study

Table 3: Discriminant function analysis pairwise Mahalanobis and Procrustes distances between sexes and regions within clusters D1, D2, D3, V1 and V2. Associated *p*-values generated from permutation tests (1 000 permutations). F = female; M = male; CT = cold-temperate; ST = subtropical; WT = warm-temperate

Groups	Mahalanobis distance	<i>p</i> -value	Procrustes distance	<i>p</i> -value
<i>Cluster D2</i>				
F–M	0.764	0.013	0.005	<0.001
CT–ST	1.137	0.166	0.006	0.334
CT–WT	1.430	0.198	0.006	0.316
ST–WT	1.528	0.866	0.003	0.687
<i>Cluster D3</i>				
F–M	1.348	0.230	0.007	0.175
CT–ST	1.428	0.909	0.007	0.838
CT–WT	2.930	0.864	0.008	0.856
ST–WT	1.791	0.174	0.008	0.226
<i>Cluster V1</i>				
F–M	10.238	0.554	0.013	0.387
CT–ST	2.529	0.999	0.026	0.397
CT–WT	1.820	0.926	0.023	0.521
ST–WT	10.981	0.522	0.011	0.788
<i>Cluster V2</i>				
F–M	0.609	0.246	0.005	0.070
CT–ST	1.329	0.012	0.008	0.060
CT–WT	1.570	0.117	0.007	0.262
ST–WT	0.892	0.162	0.005	0.349

not more likely to be found in a particular group of the other aspect. The fact that a multivariate analysis did not reveal a non-overlapping morphological cluster indicates that the great majority, if not all, of the specimens analysed belong to the same species. The normally distributed continuum of the rostral-length/zygomatic-width ratios in our sample provide further support of this interpretation in relation to the presence of longer-beaked and shorter-beaked morphotypes. This is in contrast with results obtained in a separate study of *Tursiops* spp. from South Africa (Ngqulana et al. 2019), which provided more support for putative

clusters, because the results for the dorsal and ventral aspects significantly mirrored one another.

Samaai et al. (2005) previously assessed the cranial and external morphology of *Delphinus* specimens from South Africa. Principal component analysis revealed three outliers in which the rostral length to zygomatic width fell within the range of *D. delphis* from the North Pacific (Heyning and Perrin 1994); interestingly, all three specimens were found along the South African west coast (Samaai et al. 2005). The rostra of these three individuals were significantly shorter than those typical of *Delphinus* from South Africa. In an earlier study examining the taxonomy of *Delphinus* from southern Africa, animals from this region were characterised by narrower crania and slightly longer rostra when compared with specimens from the North Atlantic (Ross 1984). Ross (1984) suggested that a longer rostrum is an adaptation associated with aspects of a shallow-water habitat. Murphy et al. (2006) also used the ratio of the rostrum length to zygomatic width to clarify the taxonomy of *Delphinus* in the eastern North Atlantic. The specimens they examined overlapped in rostral-length/zygomatic-width ratio with both *D. delphis* and *D. capensis* from the North Pacific, and thus the authors concluded that these specimens were an intermediate form of *D. delphis*. Although some specimens were characterised by shorter rostra and more-rounded skulls, they could not be recognised as a particular species since they did not cluster with either. Bell et al. (2002) examined 211 *Delphinus* crania from the coast of southern Australia and concluded that the greater range of variation within their specimens, as compared with either *D. delphis* or *D. capensis* from the eastern North Pacific, confirmed a single though morphologically variable species. Although the methods used in the current study were different to those used in previous studies, the differences or, lack thereof, reported are in concordance with the findings of Bell et al. (2002).

Sexual dimorphism

Sexual dimorphism with regard to cranial size and shape has been reported extensively for the genus *Delphinus*,

with males typically being larger than females (Murphy 2004; Murphy et al. 2006; Murphy and Rogan 2006; Esteves and Oviedo 2007; Nicolosi and Loy 2010; Jordan 2012). Differences between sexes in size and shape of the cranium are thought to be influenced primarily by mechanisms such as foraging and social behaviour; however, locomotion, balance and sound reception are other mechanisms influencing cranial shape and size differences between the sexes (Perrin et al. 2003; Marshall 2009; Rommel et al. 2009). Conry et al. (2016) found that significant differences in cranial shape between female and male striped dolphins *Stenella coeruleoalba* from South African waters involved characters of the posteriormost region of the crania and most muscle and ligament attachments. In addition, they suggested these differences might be due to differences in foraging strategies, behaviour and vocalisation. Sex-specific differences in feeding ecology might lead to differences in rostrum width and degree of robustness. Morphological differences might, however, also be associated with competitive interactions, with greater aggression by males potentially selecting for more-robust rostra (Jordan 2012). This might also explain the broader rostra of males compared with those of females. Aggression in male–male competition has been reported in both bottlenose and common dolphins (Parsons et al. 2003; Murphy et al. 2005; Scott et al. 2005). However, in terms of diet, no significant differences between the sexes were reported for *D. capensis* from KwaZulu-Natal (Ambrose 2010), which supports the hypothesis that differences in rostral width and length between sexes are more likely to be shaped by interference competition between males rather than by different feeding strategies.

The posteriormost region (exoccipital bone) of the cranium was another sexually dimorphic feature in the present study. This pattern was also observed in Dall's porpoise *Phocoenoides dalli* from California, and there the differences were interpreted as a result of sexual selection (Frandsen and Galatius 2013). This region of the cranium is known to play a pivotal role in locomotion in cetaceans and also serves as an attachment site for epaxial muscles, which are responsible for the movement of appendages, such as the flukes (Mead and Fordyce 2009; Thewissen 2009). The exoccipital condyles serve to position the head on the neck and are also responsible for some flexibility at the terminal end of the neck (Rommel et al. 2009). Thus, males may require crania that will provide for the attachment of larger neck muscles (Frandsen and Galatius 2013). It has also been suggested that these features provide the advantage of a greater range of movement of the neck during male–male aggressive interactions (Rommel et al. 2009).

Geographic variation

Significant intraspecific geographic morphological variations have been reported for a number of delphinid species (e.g. Perrin 1984, 2009; Schnell et al. 1986; Amaha 1994; Perrin et al. 2003; Westgate 2007; Loy et al. 2011). Such variation is important as it provides a basis for the description of stock units or subpopulations, which can assist in the assessment and management of appropriate units (Schnell et al. 1986). Geographically linked variation was likewise found in

this study. While none of the clusters revealed significant differences in cranial shape between the three regions, and Clusters D1, V1 and D3 did not reveal any substantial cranial size differences, such differences were significant in Clusters D2 and V2. A geographic gradient in cranial size variation was observed in these differences: specimens from the cold-temperate region were significantly larger than specimens from the other two regions, whereas specimens from the warm-temperate region were of intermediate size and specimens from the subtropical region were significantly smaller.

Geographic variation in the morphology of *Delphinus* has been found elsewhere (Perrin 2009; Galatius et al. 2012; Jedensjö et al. 2017). Variations have been suggested to correlate with adaptations to the local environment, which may differ even over short distances (Perrin 2009; Galatius et al. 2012; Jedensjö et al. 2017). Murphy et al. (2006) examined 393 crania from the eastern North Atlantic to investigate geographic variation. Whereas their results on the ratio between rostral length and zygomatic width did not reveal any significant differences between geographic areas, multivariate analysis indicated significant geographic variation among mature males and mature females (Murphy et al. 2006). Amaha (1994) found that sex-based-size-dimorphic features differed between geographic populations in common dolphins. Cranial morphology was also used to investigate geographic variation in *Delphinus* species from the North Atlantic, where it was found that a high degree of morphological variability was not systematically related to geographic location (Westgate 2007).

Inshore (coastal) and offshore morphological variation has been reported in delphinid genera, such as *Stenella*, *Tursiops* and *Delphinus* (Perrin 1975; Perrin et al. 2011; Pinela et al. 2011). Significant differences in rostral dimensions between inshore and offshore *S. longirostris* suggested that a robust feeding apparatus could be favourable when pursuing larger, demersal prey in shallow waters, whereas a small feeding apparatus might be advantageous in catching fast-moving pelagic prey (Perrin 1975). Characters associated with feeding, such as the rostrum, temporal fossa and mandibular condyle in the coastal form of *T. truncatus* in California waters, were reported to be larger than those in the offshore form (Perrin et al. 2011). In *Delphinus*, Pinela et al. (2011), in correlating rostral length with levels of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes, found that the longer-beaked common dolphins from the North Atlantic either fed at higher trophic levels or inhabited offshore waters. In contrast, Samaai et al. (2005) reported that parasite and stomach-contents data showed that long-beaked dolphins off South Africa had a more inshore habitat than short-beaked dolphins.

In some instances the extent of differences between sexes might vary geographically and these differences are mostly correlated to environmental conditions (Bell et al. 2002). For example, environments with lower productivity potentially result in poor dimorphic development (Amano and Miyazaki 1996). The west coast of South Africa is a region where upwelling occurs, which enables higher productivity than the adjacent warm-temperate and subtropical regions

(Ansorge and Lutjeharms 2007). The larger crania in the cold-temperate region might be attributable to both colder temperatures and high productivity (Ansorge and Lutjeharms 2007). Other studies have observed similar patterns (Amano and Miyazaki 1992; Baker et al. 2002; Waas et al. 2012; Duras et al. 2014). Geographically linked drivers of morphological variation in marine mammals might be differences in trophic ecology between groups, as well as habitat characteristics, such as water depth and temperature (Jedensjö et al. 2017).

In contrast to previous findings about taxonomic resolution elsewhere, the analyses of cranial morphology revealed little differentiation among the *Delphinus* spp. from South Africa. The *D. capensis* holotype clustered with the larger group (Cluster D2), indicating that most specimens from this study belong to the long-beaked form. A further study that includes molecular and external morphometric analyses would help clarify the taxonomy of *Delphinus* spp. from South Africa. Stable isotope analysis could also be used to explore the ecological diversification of *Delphinus* in South Africa.

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Appendix: Descriptive statistics for centroid sizes in crania of *Delphinus* spp., for both the dorsal and ventral aspects

	<i>n</i>	Average centroid size	SD	Median	Range
<i>Dorsal aspect</i>					
Females	146	57.9	1.7	57.8	52.5–63.4
Males	136	60.3	2.0	60.2	54.4–65.1
Cold-temperate	25	60.0	2.2	59.9	56.3–64.1
Subtropical	204	58.9	2.1	58.9	52.6–64.8
Warm-temperate	53	59.3	2.6	59.4	54.4–65.1
Cluster D1	10	60.9	1.4	60.5	59.2–63.5
Females	3	60.5	1.2	60.5	59.2–61.6
Males	7	61.1	1.5	60.6	59.3–63.5
Cold-temperate	1	60.5	–	–	–
Subtropical	8	60.9	1.5	60.5	59.2–63.5
Females	3	60.5	1.2	60.6	59.2–61.6
Males	5	61.2	1.8	60.4	59.3–63.5
Warm-temperate	1	60.8	–	–	–
Cluster D2	218	59.4	2.2	59.2	52.5–65.1
Females	121	58.1	1.6	57.9	52.5–63.4
Males	97	60.9	1.8	60.8	56.2–65.1
Cold-temperate	18	60.8	1.8	60.5	58.0–64.1
Females	8	59.3	0.8	59.4	58.0–60.6
Males	10	62.0	1.4	62.3	59.6–64.1
Subtropical	160	59.1	2.1	59.0	52.5–64.8
Females	93	58.0	1.6	57.9	52.5–63.4
Males	67	60.5	1.7	60.3	56.2–64.8
Warm-temperate	40	59.8	2.6	59.9	54.4–65.1
Females	20	58.1	1.8	57.9	54.4–61.1
Males	20	61.5	2.1	61.3	57.7–65.1
Cluster D3	54	57.7	1.8	57.5	54.4–61.5
Females	22	56.6	1.5	56.6	54.6–60.3
Males	32	58.5	1.6	58.8	54.4–61.5
Cold-temperate	6	57.3	0.6	57.3	56.3–58.2
Females	2	57.3	0.2	57.3	57.2–57.4
Males	4	57.2	0.8	57.2	56.3–58.2
Subtropical	36	57.9	1.9	58.2	54.4–61.5
Females	15	56.5	1.4	56.5	54.6–60.3
Males	21	58.9	1.6	59.0	54.4–61.5
Warm-temperate	12	57.6	1.9	57.5	54.8–61.0
Females	5	56.7	1.9	56.4	54.8–59.7
Males	7	58.2	1.8	58.2	55.5–61.0
<i>Ventral aspect</i>					
Females	132	56.1	1.9	55.8	51.8–62.6
Males	128	57.2	2.1	57.2	52.5–62.6
Cold-temperate	25	57.6	2.1	57.2	54.4–62.6
Subtropical	192	56.4	1.9	56.4	52.5–61.6
Warm-temperate	43	57.0	2.5	56.7	51.8–62.6
Cluster V1	18	55.7	2.1	56.0	52.5–59.0
Females	6	55.1	1.9	55.3	52.7–57.7
Males	12	55.9	2.2	56.4	52.5–59.0
Cold-temperate	1	55.0	–	–	–
Females	–	–	–	–	–
Males	1	55.0	–	–	–
Subtropical	12	55.9	2.4	56.5	52.5–59.0
Females	4	55.2	2.1	55.3	52.7–57.7
Males	8	56.2	2.6	57.4	52.5–59.0
Warm-temperate	5	55.2	1.6	56.2	53.1–56.6
Females	2	54.8	2.4	54.8	53.1–56.5
Males	3	55.5	1.5	56.2	53.9–56.6
Cluster V2	242	56.7	2.1	56.7	51.8–62.6
Females	126	56.1	1.9	55.8	51.8–62.6
Males	116	57.4	2.0	57.3	52.8–62.6
Cold-temperate	24	57.8	2.1	57.4	54.4–62.6
Females	9	58.6	2.2	58.3	54.9–62.6
Males	15	57.3	2.0	57.0	54.4–61.7
Subtropical	180	56.5	1.9	56.4	52.5–61.6
Females	98	55.9	1.7	55.6	52.5–60.6
Males	82	57.2	1.9	57.3	52.8–61.6
Warm-temperate	38	57.2	2.5	57.4	51.8–62.6
Females	19	56.3	2.2	56.0	51.8–60.2
Males	19	58.2	2.5	58.0	54.0–62.6