Osteological variation in the spectacled porpoise (*Phocoena dioptrica*)

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ABSTRACT

Cranial and post-cranial variation is described for a large series of specimens of spectacled porpoise from Argentina and compared with that for specimens from other areas of the Southern Hemisphere. Condylobasal length in 54 adult skulls was 276-424. Tooth counts were 16-26 and 17-23 in the upper and lower jaws, respectively. Total number of vertebrae ($n = 20$) was 66-70. The rostrum may be relatively smaller in the Auckland Islands than in other regions.

KEYWORDS: SPECTACLED PORPOISE; SOUTHERN HEMISPHERE; MORPHOMETRICS; STOCK IDENTITY

INTRODUCTION

Before Goodall began her systematic collections of beached remains of marine mammals along the southern coasts of Argentina and Chile in the mid-1970s (Goodall, 1978), there was little available information on the spectacled porpoise (*Phocoena dioptrica*). Only a handful of specimens existed in the world's museums, and even fewer had been documented in the literature. Brownell (1975) summarised knowledge of the species, including osteological data reported by Lahille (1912), Marelli (1922), Hamilton (1941) and Praderi (1971). Data on additional specimens have been reported subsequently by Baker (1977), Goodall (1978), Goodall and Cameron (1979), Guiler *et al.* (1987, as *Phocoena spinipinnis*, see Brownell, R.L. *et al.*, 1989), Goodall and Schiavini (1995) and Brownell and Clapham (1999). The skull was illustrated by Brownell (1975), Goodall (1978) and Brownell and Clapham (1999) and the post-cranial skeleton by Brownell (1975) and (in part) Goodall and Cameron (1979). Much more material is now available, and the purpose of this paper is to describe individual and geographic variation in the skull and post-cranial skeleton based on the larger series of specimens.

MATERIALS AND METHODS

The new sample consisted of 111 osteological specimens, ranging from only a few isolated bones (e.g. the fused cervical vertebrae) to complete skeletons with data on sex and length, all from southern Argentina (Appendix 1).

A major problem was how to decide which specimens to include in the 'adult' series for cranial measurements. Very small skulls with obvious juvenile characteristics (e.g. unankylosed maxillae, frontals and other major elements) were easily identified as non-adults. However, no characteristics that clearly and consistently separated sub-adults from adults were found. The specimens were therefore allocated to 'adult' and 'non-adult' series based on condylobasal (CB) length and the few available data on sexual and physical maturity. Perrin and Heyning (1993) noted that cranial maturity (cessation of elongation of the skull) is attained in at least some small odontocetes at approximately the time of sexual maturation and before the onset of physical maturity (cessation of increase in body length, signalled by fusion of all vertebral epiphyses to the centra). Data on sexual maturity existed for four specimens (two males and two females) and on physical maturity for 27 specimens ranging from 262-324mm in CB length. A male of CB length 276mm was physically mature. A female of CB length 279mm was both physically and sexually immature. The male was included in the adult series and the female and three physically immature specimens (with no information on sexual maturity, and with CB lengths of 262, 275 and 276mm) were excluded. Also excluded were skulls for specimens known to be sexually immature or of unknown maturity for which it was not possible to determine CB length because of damage to the tip of the rostrum. These criteria were used to minimise the inclusion of relatively large but immature skulls and the exclusion of relatively small but mature skulls; the adult sample for CB length included 54 specimens.

For post-cranial measurements, specimens known to be physically mature (vertebral epiphyses fused to centra) were included. This yielded a series of 22 specimens.

Measurements were taken after Perrin (1975). Most of the cranial measurements were taken by Perrin (46 specimens), with some by Cozzuol (8) and one skull measured by Alejandro Purgue (pers. comm.). The post-cranial measurements were made by Perrin (10), Purgue (9) and Cozzuol (3). Measurement technique was standardised among Perrin, Cozzuol and Purgue by inter-comparison of measurements and re-measurements of a series of specimens at the beginning of the study. CB length for one previously unpublished adult specimen was contributed by R. Praderi (pers. comm.).

Published meristic data (tooth counts and post-cranial vertebral and rib counts) were included in the sample for statistical analysis, but published cranial measurements were not, because of the potential for differences in measurement technique.

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Table 1

Statistics for cranial measurements of adult specimens of *Phocoena dioptrica* in present sample, in mm.

	Range	(*n*)	Mean	SD	CV
Condylobasal length	276-324	(54)	297.3	10.96	3.68
Rostrum					
Length	112-139	(42)	123.1	6.33	5.15
Width at base	71-92	(46)	81.8	4.38	5.35
Width at ¼ length	55-73	(50)	64.1	3.74	5.83
Width at ½ length	45-61	(47)	53.0	3.59	6.78
Width at ¾ length	36-48	(44)	40.6	3.27	8.05
PMX width at ½ length	21-37	(48)	27.3	3.06	11.30
Tip of rostrum to:					
External nares	133-176	(53)	158.5	8.71	5.49
Internal nares	151-190	(49)	166.9	8.72	5.23
Preorbital width	132-167	(45)	151.3	7.87	5.20
Postorbital width	160-188	(50)	172.9	6.84	3.96
Zygomatic width	161-190	(44)	175.8	7.41	4.21
Width of external nares	26-42	(54)	33.9	3.01	8.88
Max. width of PMXs	39-54	(53)	46.4	3.45	7.44
Parietal width	128-158	(51)	141.1	6.63	4.70
Height of braincase	90-115	(53)	101.9	5.48	5.38
Int. length of braincase	101-124	(54)	111.7	5.67	5.08
Length of temporal fossa	44-73	(50)	58.4	6.21	10.63
Height of temporal fossa	32-65	(50)	45.0	6.33	14.07
Length of orbit	47-34	(51)	55.5	3.41	6.14
Length of antorb. process	20-34	(49)	27.6	3.47	6.25
Width of internal nares	53-66	(41)	59.6	3.30	5.54
Separation of pterygoids	5-26	(22)	15.9	-	-
Length of upp. toothrow	85-111	(22)	97.3	-	-
Length of low. toothrow	75-108	(16)	91.8	-	-
Length of ramus	203-229	(18)	218.7	-	-
Height of ramus	58-68	(18)	63.9	-	-
Max. diameter of tooth	1.6-4.0	(17)	2.55	-	-

Table 2

Coefficients of variation for cranial measurements of (A) *Phocoena dioptrica* from Argentina (from Table 1), *Phocoena phocoena* from the (B) eastern North Atlantic and (C) western North Pacific (Amano and Miyazaki, 1992; sample sizes 29-39), and (D) offshore specimens of *Stenella attenuata* from the eastern tropical Pacific (Perrin, 1975; sample sizes 65-70).

	A	B	C	D
Condylobasal length	3.68	5.02	5.02	3.14
Rostrum:				
Length	5.15	6.40	6.81	4.17**
Width at base	5.35	8.39	7.22	4.34**
Width at ¼ length	5.83	9.81	7.76	-
Width at ½ length	6.78	9.98	6.98	6.96**
Width at ¾ length	8.05	9.61	7.46	9.33**
PMX width at ½ length	11.30	12.44	9.78	10.14**
Tip of rostrum to:				
External nares	5.49	6.51	7.03	4.39**
Internal nares	5.23	-	-	4.24**
Preorbital width	5.20	8.19	6.39	3.56**
Postorbital width	3.96	6.29	5.69	3.02**
Zygomatic width	4.21	6.56	5.87	3.18**
Width of external nares	8.88	8.66	8.48	4.96
Max. width of PMXs	7.44	-	-	4.38**
Parietal width	4.70	4.08	3.73	3.40**
Height of braincase	5.38	-	-	4.37**
Int. length of braincase	5.08	-	-	-*
Length of temporal fossa	10.63	7.62	9.19	6.27**
Height of temporal fossa	14.07	12.08	13.51	6.31**
Length of orbit	6.14	-	-	4.26
Length of antorb. process	6.25	-	-	6.69**
Width of internal nares	5.54	8.71	6.90	7.20**

*Measurement determined to be sexually dimorphic in *S. attenuata* by Perrin (1975). ** Subsequently determined by Schnell *et al.* (1985) to be sexually dimorphic in *S. attenuata*.

RESULTS AND DISCUSSION

The skull

Fifty-four skulls ranged from 276-324mm in CB length (Table 1). Cranial variability was less than in comparable series of specimens of the harbour porpoise (*Phocoena phocoena*) from the eastern North Atlantic and western North Pacific, but greater for most dimensions than in a series of offshore specimens of the pantropical spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific (Table 2). The latter difference is most pronounced for width of the skull and of length and height of the temporal fossa. As the specimens for the most part were not identified to sex, an unknown proportion of this variability may be due to sexual dimorphism. The lesser variability of this pelagic species compared to that of the more coastal harbour porpoise may suggest less populational sub-division because of greater individual home range or greater genetic flow across the species range within an oceanic region. Other possible factors to consider in these comparisons are population size and age, both known to correlate with genetic variability (Nei, 1987). For example, the eastern tropical pelagic populations of *Stenella* spp. are thought to possibly be of relatively recent origin (Perrin *et al.*, 1985; 1991) and thus, other factors being equal, could perhaps be expected to exhibit less genetic (and potentially phenotypic) variability than older populations of pelagic small cetaceans. Selection is another potential factor. Lesser phenotypic variability may reflect an adaptive premium on more standardised size or shape.

Table 3

Statistics for tooth/alveolus counts and postcranial meristic characters in *Phocoena dioptrica*. Includes present sample and data from Lahille (1912), Marelli (1922), Hamilton (1941), Praderi (1971) and Baker (1977). Standard deviations (SD) and coefficients of variation (CV) included for samples of 25 or more.

	Range	(*n*)	Mean	SD	CV
Tooth/alveolus counts:					
Upper left	16-25	(22)	20.5	-	-
Upper right	18-24	(22)	20.5	-	-
Lower left	17-23	(23)	18.9	-	-
Lower right	17-23	(22)	18.5	-	-
Vertebrae:					
Total number	66-70	(20)	67.3	-	-
Thoracic	13-14	(40)	13.7	0.45	0.33
Lumbar	13-16	(30)	13.6	1.04	7.64
Caudal	29-34	(14)	32.1	-	-
First with vert. for.	40-46	(30)	43.7	1.62	3.71
Last with trans. proc.	44-48	(30)	45.5	1.11	2.44
Last with neur. proc.	50-53	(30)	51.5	1.14	2.21
First with chevron	35-36	(7)	35.7	-	-
Fused cervicals	5-7	(63)	5.7	0.56	9.91
Widest vertebra	22-25	(33)	23.2	0.97	4.18
Number of ribs:					
Left vertebral	13-14	(31)	13.7	0.48	3.47
Right vertebral	13-14	(28)	13.6	0.50	3.68
Left sternal	7-9	(14)	7.5	-	-
Right sternal	7-9	(17)	7.5	-	-

Tooth counts ranged from 16-25 in the upper jaw and 17-23 in the lower jaw (Table 3), for ranges of 9 and 6 teeth, respectively. This is comparable to the range of variation found by Amano and Miyazaki (1992) in comparable samples of the harbour porpoise (22-30 upper and 21-30 lower, for ranges of 8 and 9 teeth), as well as in the earlier study by Yurick and Gaskin (1987; 21-29 upper and 20-29 lower). However, the lower end of the ranges in the spectacled porpoise may reflect missing teeth (from ill-defined or abraded alveoli). The teeth are usually

spatulate but can also be peg-like with minimally expanded cusps (Fig. 1). Some of the teeth may be apically flattened due to wear.

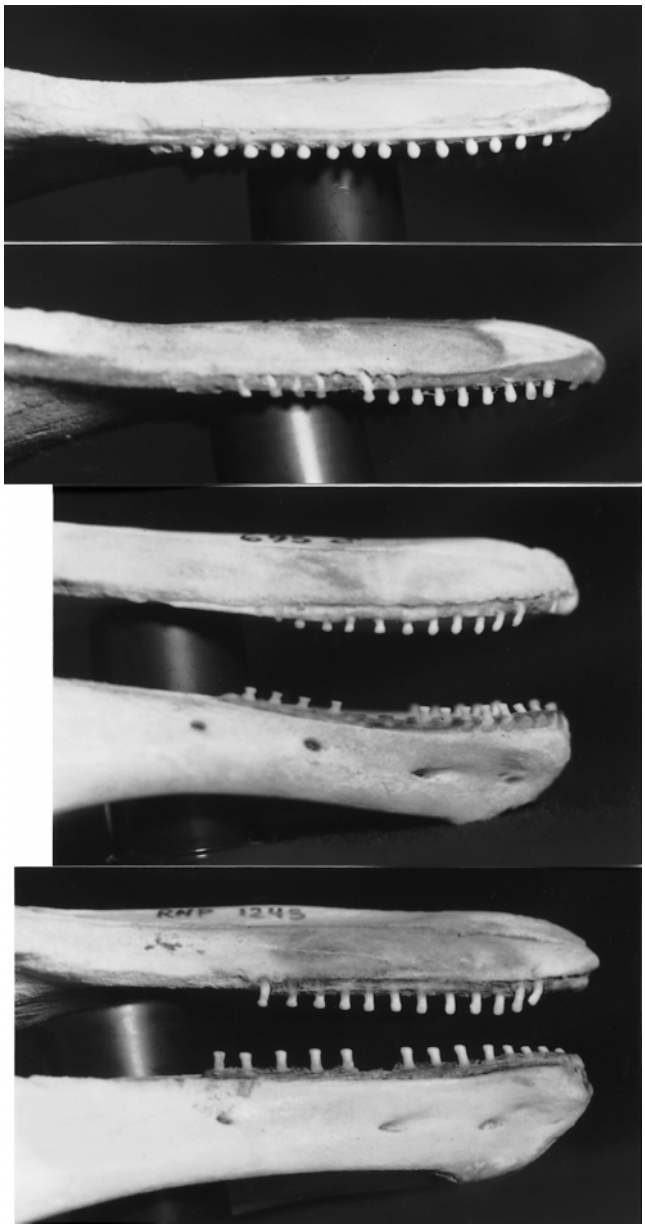

Fig. 1. Variation in tooth shape in *Phocoena dioptrica*: (top to bottom) RNP 39, RNP 1965, RNP 695 (male), RNP 1245, all from Tierra del Fuego.

The post-cranial skeleton

Although the present sample is small (20), the variation in total vertebral count (66-70) is comparable to that reported for regional series of other delphinoids, e.g. 67-72 (CV = 1.5) in 52 specimens of Atlantic spotted dolphin (*Stenella frontalis*) from the Atlantic (Perrin *et al.*, 1987), 77-83 (CV = 1.6) in 51 pantropical spotted dolphin specimens from the eastern tropical Pacific (Perrin, 1975), and 74-80 (CV = 2.0) in 80 short-beaked common dolphin specimens (*Delphinus delphis*) from southern California (Heyning and Perrin, 1994). It is lower than for the pantropical spotted dolphin worldwide (74-84 in 175 specimens, CV = 1.9; Perrin *et al.*, 1987). The greatest variation is in the number of caudals (29-34 in 14 specimens). The typical vertebral formula is C7+T14+L14+Ca32 = 67. The position of the last vertebra bearing a transverse process (44-48) and the last bearing a neural process (50-53) are very stable (CV = 2.44 and 2.21, respectively). The number of fused cervicals ranges from 5 to 7 and is highly variable (3-7, CV = 13.04).). Statistics for postcranial measurements of physically mature specimens of *Phocoena dioptrica* in the present sample are shown in Table 4.

Table 4

Statistics for postcranial measurements of physically mature specimens of *Phocoena dioptrica* in present sample, in mm (except total length of skeleton, which is in cm).

	Range	(*n*)	Mean
Atlas:			
Width of anterior face	66-83	(15)	77.1
Height	44-58	(15)	53.3
Length of lateral process	18-39	(16)	29.1
Length of neural spine	15-50	(15)	39.1
First thoracic vertebra:			
Height	54-67	(17)	60.4
Maximum width	72-96	(17)	84.7
Length of neural spine	13-46	(13)	35.6
First lumbar vertebra:			
Height	57-74	(14)	64.7
Maximum width	181-208	(12)	191.5
Length of neural spine	71-94	(11)	85.7
Length of first vertebral rib	135-168	(13)	152.5
Length of longest vertebral rib	296-341	(9)	319.1
Maximum width of manubrium	87-111	(8)	95.9
Greatest length of radius	-	(1)	70
Greatest length of ulna	-	(1)	63
Maximum width of humerus	-	(1)	35
Length of longest chevron	40-56	(7)	48.1
Greatest length of pelvic	62-107	(3)	85.0
Width of widest vertebra	186-221	(14)	200.4
Length of centrum of first lumbar	31-36	(14)	33.3
Total length of skeleton (cm)	169-205	(5)	183.8

Comparison with previously published data

The published measurements for Argentine specimens (Table 5) fall within the ranges for the present sample with a few exceptions. Marelli (1922) reported basal width of the rostrum for his specimen as 129mm, considerably above the range for all other specimens in Tables 1 and 5. His photographs of the specimen do not show it to be markedly different in form from those examined by us, and the difference must be ascribed to measurement error or to a measuring method different from that used by others.

Praderi (1971) reported basal width and half-length width of the rostrum for one of his specimens as 97mm and 62mm, respectively, slightly above the range for the present sample. Another had a rostrum length slightly below the range for the present sample, and a third had maximum skull height also slightly below the range. These small differences can be ascribed to slight differences in measuring technique.

Geographical variation

Marked differences in skull measurements have been found for the closely related harbour porpoise between ocean basins and even between opposite sides of the North Atlantic (Yurick and Gaskin, 1987; Amano and Miyazaki, 1992), and it would not be surprising to find such variation within the broad range of *P. dioptrica*. The sample sizes are very small for other than southern Argentina, but some patterns are suggested.

Table 5

Published cranial measurements (in mm) of adult specimens of *Phocoena dioptrica* from Argentina (A, Marelli, 1922; B, Praderi, 1971, sample size four unless otherwise noted), Falkland Islands/Islas Malvinas (C, Hamilton, 1941), Enderby Island in Auckland Islands (D, Baker, 1977) and Heard Island (E, Guiler, 1987).

	A	B	C	D	E
Condylobasal length	315	285-295	288	310	303
Rostrum:					
Length	-	110-125	121	117	162*
Width at base	129*	79-97	88	84	82
Width at ½ length	57	54-62	-	51	51
Width at ¾ length	-	-	-	38	38
PMX width at ½ length	-	-	32	29	31
Preorbital width	-	-	155	162	164
Postorbital width	153	-	170	-	-
Zygomatic width	-	153-171	168	-	169
Max. width of PMXs	-	45-52(3)	45	45**	-
Parietal width	-	-	143	157	156
Length of temporal fossa	-	42-48	-	61	42
Height of temporal fossa	-	34-36	-	58	39
Length of upp. toothrow	92	84-95	-	81	79
Length of low. toothrow	-	82-96	-	-	-
Length of ramus	-	213-225(3)	-	-	-
Height of ramus	-	59-60(2)	-	-	-
Max. diameter of tooth	-	-	-	3.0	-
Max. height of cranium	-	132-144(3)	-	155	163

* Erroneous values (see text).
** Corrected from value of 78mm in Baker (1977).

The Falklands/Malvinas specimen falls within the range for the mainland Argentine series in all measurements. Guiler *et al.* (1987) reported length of the rostrum for the Heard Island specimen as 162mm, far above that reported for any other specimen. This is an error; measurement of the rostrum in the published photograph of the skull yields a value of approximately 123mm, within the range for other specimens. Tooth counts (14/13) and length of upper tooth row (71/79) are below the ranges for other specimens, but it appears in the photograph that the proximal portion of the rostrum was severely abraded latero-ventrally, obliterating the posterior ends of the rows of alveoli and yielding artificially low alveolus counts and tooth row lengths.

The Auckland Islands specimen appears to differ significantly from the other series in two features. The rostrum is relatively very small (117mm vs CB length of 310mm, for a ratio of 0.377, as opposed to a range of 0.381-0.443 and an average of 0.413 in the 52 adult Argentine skulls in the present sample). The length of the upper tooth row (81mm) falls below the range of 85-111mm in the Argentine sample of 28 (Tables 1 and 5). It is possible that this reflects a smaller rostrum size in the Auckland Islands population than in the others.

Larger samples from throughout the range of the species will be necessary to allow confirmation of the geographical patterns of variation suggested by the present material.

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APPENDIX 1

SPECIMENS OF *PHOCOENA DIOPTRICA* EXAMINED

Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina (CNP) 116; Instituto Tecnológico de Estudios Superiores de Monterey, Guaymas, Mexico RNP 429, 757; Instituto de Zoología, Universidad Austral, Valdivia, Chile (IZUA) RNP 65; Los Angeles County Museum (LACM) 86042 (RNP 1146), 86043 (RNP 583); Museo Acatushún de Aves y Mamíferos Australes, Harberton, Tierra del Fuego, Argentina RNP 10, 18, 33, 38, 39, 41, 46, 71, 82, 83, 85, 98, 99, 123, 125a, 131, 146, 174, 194, 195, 205, 221, 232, 234, 267, 268, 281, 292, 297, 299, 301, 318, 324, 363, 364, 376, 401, 412, 431, 438, 440, 443, 448, 449, 454, 455, 460, 463, 464, 469, 494, 505, 533, 536, 589, 600, 609, 621, 625, 658, 690, 694, 695, 737, 750, 759, 770, 776, 870, 896, 906, 969, 1000, 1008, 1013, 1014, 1018, 1084, 1095, 1196, 1220, 1245, 1313, 1333, 1348, 1353, 1461, 1465, 1481, 1547, 1615, 1622; Museo Nacional de Historia Natural de Montevideo (MNHN-M) RNP 525; Museo de La Plata (MLP) 1201, 1202; Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) 20491 (RNP 525), 20492 (RNP 732), 20493 (RNP 298), Ad-1; Museum of New Zealand Te Papa Tongarewa (MNZ) 1977 (RNP 970), 1978 (RNP 599); Southwest Fisheries Science Center (SWFC) 0122 (RNP 319); US National Museum of Natural History (USNM) 571485, 571486, 571487 (RNP 36, 1030, 1061).