

GEOGRAPHICAL VARIATION IN SKULL MORPHOLOGY OF THE IRRAWADDY DOLPHIN, *ORCAELLA BREVIROSTRIS* (OWEN IN GRAY, 1866)

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ABSTRACT. – Analysis of skull morphology of Irrawaddy Dolphin *Orcaella brevirostris* specimens from throughout its range resulted in significant separation of specimens from Australia (including one specimen from Papua New Guinea) and those from Asian countries. Specimens from Australia were characterised by a range of nodular nasal ossicles (vs. two transversely elongate, antero-posteriorly compressed nasal bones in Asian specimens); a reduced mesethmoid plate, widely separated from the nasal ossicles by exposed frontal bones (vs. well developed mesethmoid plate, adjacent to, or contacting the nasal bones); and narrowly separated pterygoid hamuli (vs. widely separated). The Australian specimens showed a more derived cranial osteology, suggesting an origin from Asian populations – possibly during an episode of lowered sea level – with subsequent genetic isolation of the Australian populations. The results from this study indicate a taxonomic separation of Australian specimens at the subspecies or even species level, but no formal proposal is made, pending further study using both morphological and molecular characters.

KEY WORDS. – Irrawaddy dolphin, *Orcaella brevirostris*, cranial osteology, geographical variation, taxonomy, systematics.

INTRODUCTION

The Irrawaddy dolphin *Orcaella brevirostris* (Owen in Gray, 1866) is a small delphinid that occurs in the tropical/subtropical Indo-west Pacific, from the northwest Bay of Bengal to northeastern Australia (Stacey & Arnold, 1999). Preliminary abundance estimates for *Orcaella* suggest that populations throughout its range in Asia are small and many may be declining (Dhandapani, 1992; Stacey & Leatherwood, 1997; Krebs, 1999; Smith & Hobbs, 2002; Beasley et al., 2002). Only in northern Australia have substantial populations been documented (Freeland & Bayliss, 1989), leading Perrin et al. (1996) to advocate significant conservation efforts in that region. While such efforts are important in their own right, the concept of Australia as a single refuge rests on the assumption that *Orcaella* is represented by a single taxonomic entity throughout its range. Preliminary information from our research suggests that this may not be the case.

Anderson (in Gray, 1871) described a new species, *Orcaella fluminalis*, from the Ayeyarwady [Irrawaddy] River, Burma [Myanmar], which has also been recognised as the subspecies *O.b. fluminalis* Ellerman & Morrison-Scott, 1951.

Subsequent researchers (e.g. Lloze, 1973; Pilleri & Gihl, 1973-1974) have failed to find features supporting recognition of these taxa. Presently, only the species *O. brevirostris* and the nominotypical subspecies *O. b. brevirostris* are recognised as valid (Rice, 1998).

Arnold & Heinsohn (1996) examined the cranial osteology of 18 Australian specimens and compared these with descriptions and figures of 10 Asian specimens in the literature (Owen, 1866; van Beneden & Gervais, 1868-1879; Anderson, 1879; Fraser & Purves, 1960; Pilleri & Gihl, 1973-1974). They commented on differences in the vertex, including multiple nasal bones (referred to as ‘ossicles’ in the present paper) in Australian specimens (vs. two, transversely elongate nasal bones in Asia), reduced mesethmoid plate (vs. well defined mesethmoid plate, abutting on or close to the nasal bones in Asia) and narrow separation of the pterygoid hamuli (vs. widely separated pterygoid hamuli in Asia).

In a phylogenetic study of delphinid cetaceans, LeDuc et al. (1999) analysed the full cytochrome B sequences of two *Orcaella* specimens, one from northeastern Australia (marine habitat) and the other from the Mekong River, Lao P.D.R.

(freshwater habitat). A high degree of genetic differentiation (5.3%) was found between the samples. However, it is impossible from this result to separate geographical (Australia/Laos) variation from habitat (marine/freshwater) variation.

Our study assesses intraspecific variation in skull morphology based on re-examination of specimens from the whole range of the species. The larger sample size, including specimens from both marine and freshwater habitats in Asia, allows a preliminary assessment of geographical and habitat factors. These results, with a collaborative DNA-based study (to be reported separately), allow investigation of genetically distinct stocks of *Orcaella* – a research topic identified as high priority by Stacey & Leatherwood (1997) and the International Whaling Commission (2001).

MATERIALS AND METHODS

We examined a total of 124 cranial specimens held at various museums, institutes, whale temples and universities, from throughout the species' range (including riverine, lacustrine and coastal marine specimens – Fig. 1, Appendix 1). Photographs were taken of the dorsal, ventral and lateral

aspects of the skull, as well as close ups of the vertex and pterygoid region. However, for seven specimens (one from the Dhakka Museum, Bangladesh, and six from Don Det Temple, Vietnam) only photographs were available and only qualitative features were noted. These seven specimens were not included in any subsequent analyses. Of the remaining 117 skulls, 98 were complete and considered to be cranially mature, based on complete fusion of all bones (nine were rejected, based on a lack of fusion of maxillary and frontal bones and ten were rejected based on a complete lack of frontal bones).

We adopted a subset of measurements from Perrin (1975) (Fig. 2, Table 1). An additional set of measurements were taken after Arnold & Heinsohn (1996). These included: length and width of nasal bones/depressions, separation between posterior margin of mesethmoid plate and antermost nasal bone/ossicle, minimum and maximum distance between pterygoid hamuli and depth of pterygoid region (Fig. 2, Table 1). In 80 of the 98 specimens examined, the nasal bones had been lost, but distinct depressions from the bones remained. In these cases, the widths and lengths of the nasal bones were taken using measurements of the depressions. In Australian specimens, the depressions could be further divided by bony partitions, indicating that there

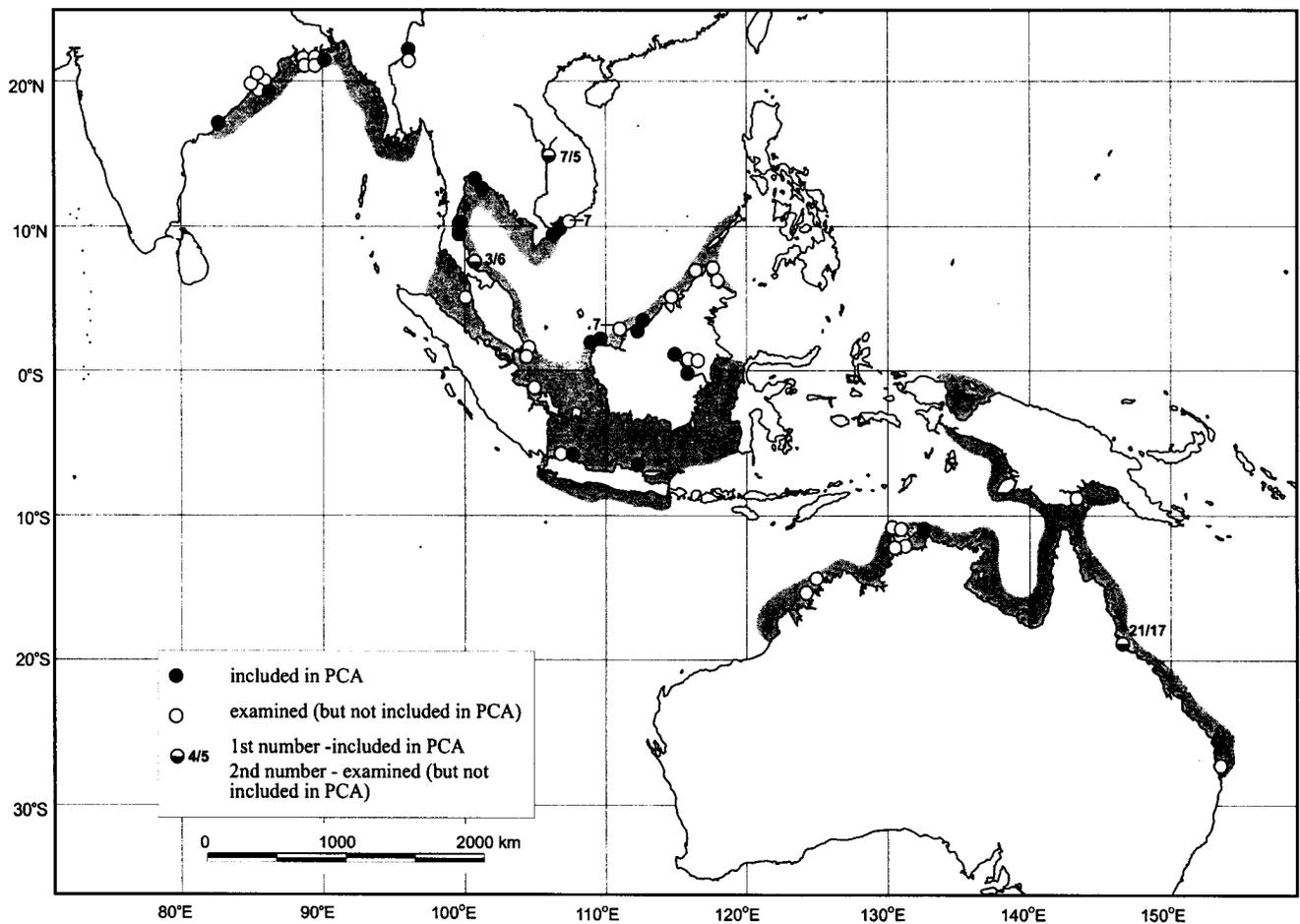


Fig. 1. Map of Australia and Asia showing the range of *Orcaella* (shaded) based on literature records and the distribution of collection localities for the specimens examined in this study.

The specimen MCZ5321 (Victoria, Australia - Appendix 1, 175) was mislabelled and originated from an unknown location in Australia. This specimen is excluded from the location map.

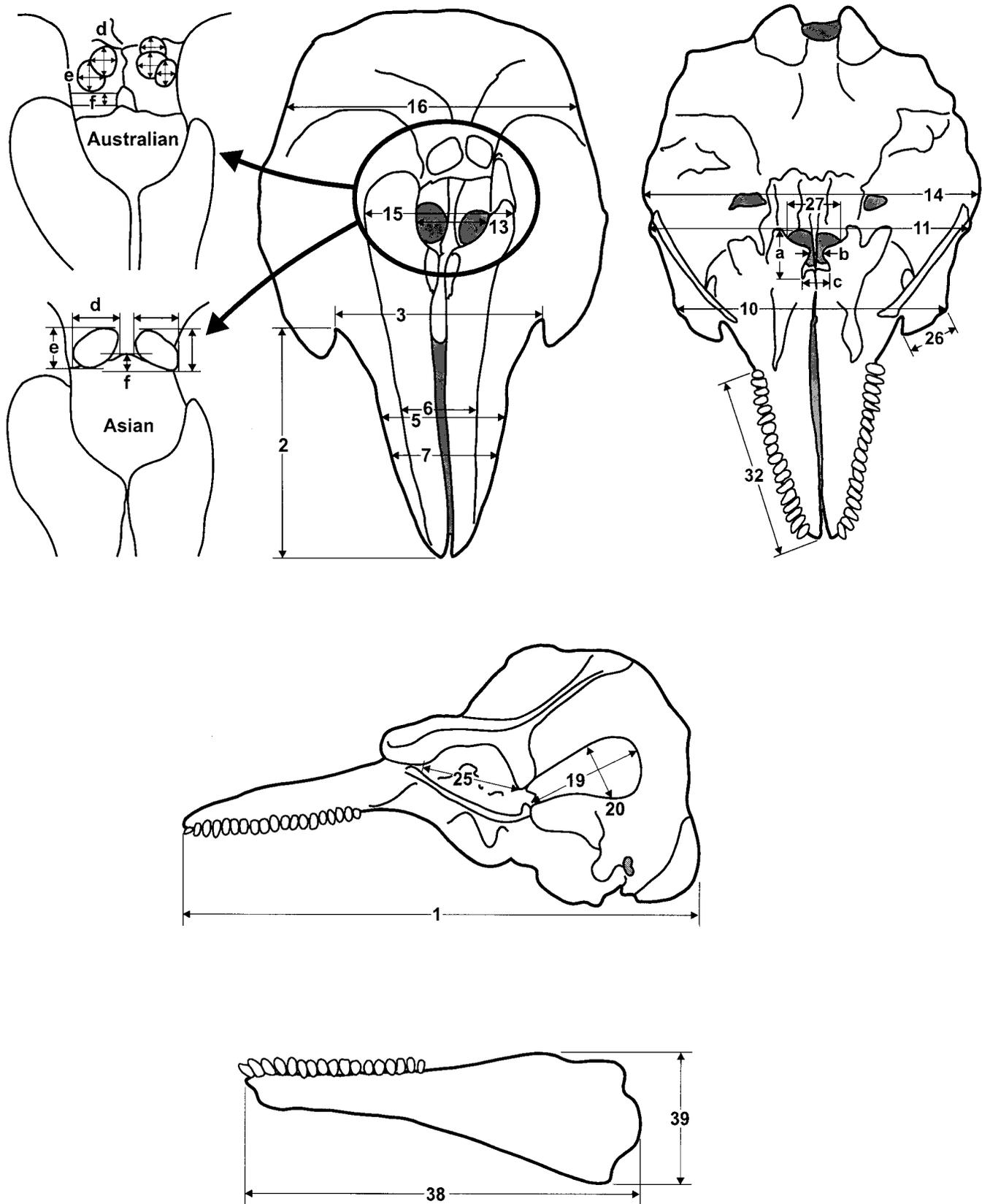


Fig. 2. Measurements taken on *Orcaella* skulls. The number refers to measurement as given in Perrin (1975); this number is shown in bold and in parentheses in Table 1. The letters refer to additional measures from Arnold & Heinsohn (1996), as indicated in Table 1.

had been two or more discrete bones or ossicles within the depressions. These were used to indicate the number and sizes of the ossicles. Nasal bones were retained in a sufficient number of *Orcaella* skulls to establish that cranial depressions are good indicators of the nasal bone/ossicle length and width. All measurements were taken from the left side of the skull. All skulls were measured using either an Anthropometer (a type of vernier caliper) or standard vernier calipers. A total of 96 specimens were measured by the senior author and two (one from Malaysia and one from Australia) by T.A. Jefferson. Previous interobserver measurement calibration had been undertaken on twelve *Orcaella* specimens to ensure consistency of measurements.

Australia/Papua New Guinea Specimens

Forty-seven skulls originated from Australia/Papua New Guinea (four partial and 43 complete). The distribution of specimens covers most of the range of *Orcaella* in Australia, including: two from Western Australia, five from the Northern Territory, 38 from Queensland (including a specimen from the Brisbane River, the most southerly record of *Orcaella* (Paterson et al., 1999)) and one specimen from an unknown location (MCZ5321, Appendix 1, 175). This specimen was labeled as originating from Victoria, Australia, which is well outside the range of *Orcaella*. The skull was probably mislabelled when exported to America (where some

Table 1. Measurements and counts taken on *Orcaella* skulls, with the subset of characters used in the PCA marked by asterisks '*'. The bold number in parentheses after each standard measure refers to the corresponding measurement in Perrin (1975); it is this number which is used in Fig. 2, showing how measurements were taken. Additional measurements are from Arnold & Heinsohn (1996); the bold letter in parentheses refers to Fig. 2, which shows how these measurements were taken on specimens from Australia and Asian countries respectively.

Measurements/count	Principal Components Analysis
1. Condylobasal length (1)	*
2. Length of Rostrum (2)	*
3. Width of Rostrum at base (3)	*
4. Width of rostrum at 1/2 length (5)	*
5. Width of rostrum at 3/4 length (7)	*
6. Width of premax. at 1/2 length (6)	*
7. Greatest width of premax. (15)	*
8. Preorbital width (10)	*
9. Postorbital width (11)	*
10. Zygomatic width (14)	*
11. Parietal width (16)	*
12. Width of external nares (13)	*
13. Width of internal nares (27)	*
14. Length of temporal fossa (19)	*
15. Height of temporal fossa (20)	*
16. Length of orbit (25)	*
17. Length of antorbital process (26)	*
28. Length of upper toothrow (32)	*
29. Length of mandible (38)	*
20. Height of mandible (39)	*
21. Length of mandibular symphysis (•)	*
22. Tooth Counts UR UL LR LL ©	*
23. Tooth Diameter (middle LL) (•)	*
TOTAL	13
Additional Measurements	
24. Depth of pterygoid region (a)	*
25. Minimum width between (b) pterygoid hamuli	*
26. Maximum width between (c) pterygoid hamuli	*
27. Number of nasals (#NASALS) ©	*
28. Length of right nasal	*
29. Width of right nasal	*
30. Length of left nasal (d)	*
31. Width of left nasal (e)	*
– average length of nasal	*
– average width of nasal	*
32. Separation between posterior margin of mesethmoid plate and anteriormost nasal bone/ossicle (f)	*
TOTAL	7

• These measures are not indicated on Figure 2.
 © These measures are counts and are not indicated in Figure 2.

early specimens have information only on the Australian port of export). Therefore, although this specimen originates from Australia, the exact location remains unknown (Rutzmoser pers. comm.). One skull from Daru, Papua New Guinea (PNG), was examined. It was kept separate from Australian specimens in the univariate analysis, although it could possibly have been caught within Australian territorial waters in Torres Strait (Fig. 1). All specimens from Australia/Papua New Guinea (hereafter referred to as 'Australia' only) were of marine origin.

Asian Specimens

We measured 70 skulls from Asia (15 partial and 55 complete), originating from Malaysia (14 marine), Thailand (nine lacustrine and four marine), Cambodia (12 riverine), Vietnam (nine marine), India (five brackishwater-lake and five marine), Indonesia (three riverine and four marine), Singapore (two marine), Burma (two riverine), Brunei (one marine). These include the type of *O. brevirostris* (BM1865.4.20.1) and one of the specimens (BM1877.12.10.17) donated by Dr. J. Anderson, apparently used in the account of *O. fluminalis* osteology in his monograph (Anderson, 1879). Sclater (1981) lists a specimen (without registration number, Appendix 1 - 162) from the Indian Museum (Calcutta) as being collected at Bhamo, [Burma] by 'Capt Bowers, 1870'. If this information can be confirmed, that specimen would be the type of *O. fluminalis*. This specimen was examined by the senior author, however there remains some question about whether the registration number in the Indian Museum refers to the skull (which is now in three sections) or just to post-cranial material (found with the skull), to which the label was attached. The specimen is incomplete and was therefore excluded from the multivariate analysis. Of the 55 complete skulls, 32 were of marine origin and 23 were of freshwater origin (13 riverine and 10 lacustrine - three of the lacustrine specimens were from brackish water in Chilka Lake, India).

Allocation of Specimens to Habitat

For analysis of geographical variation, we grouped specimens by country of origin. Additional information was required to classify specimens as marine, lacustrine or riverine. The specimens originating from Songkhla Lake, southern Thailand, were classified as freshwater-lacustrine due to the population's potentially restricted distribution in the upper, freshwater portion of Thale Luang, Songkhla Lake (Beasley et al., 2002). Three specimens from Chilka Lake, India, were classified as lacustrine, as they were found in the brackish waters of the lake (Dhandapani, 1992; Sahu et al., 1998). The lacustrine specimens were separated from marine specimens for the analyses, as the extent of movement into marine waters (if any) of lacustrine animals is presently unknown.

Cambodian specimens from the Mekong River and all specimens from the Mahakam and Irrawaddy [Ayeyarwady]

Rivers were classified as riverine. Specimens from Vietnam were obtained from Vung Tau, a small coastal town bordering the edge of the Mekong River Delta. Although the sites of collection for these specimens are unknown, it can be assumed from temple keeper reports that they were found near the town or even partway downstream into the Delta. There is a possibility that some of the carcasses could have floated downstream from the Mekong River, however, the influence of the coastal marine water extends considerably inside the Delta from the Vung Tau area. These specimens were categorised as 'marine' because there is a much higher probability that the dolphins were from coastal marine waters, rather than being from freshwater. Although the country of origin is certain, caution needs to be applied when assessing the results of habitat variation for the Vietnam specimens.

The specimen collected near the mouth of the Brisbane River, Queensland, Australia, is considered marine, as there are no exclusively freshwater populations of *Orcaella* in Australia.

Statistical Analyses

Statistical analyses were performed on data taken from intact, or nearly intact skulls (i.e., the rostrum and brain case could not be missing significant portions) of animals we judged to be cranially mature (discussed above). Multivariate statistics were used to examine the samples for geographic and habitat variation. Principal Components Analyses (PCA) were conducted using the statistical software package PCORD, version 4.0 (McCune & Mefford, 1999). The PCAs were run using a correlation matrix with no additional rotation. Multivariate analyses are known to be sensitive to missing data, therefore the PCAs were restricted to specimens with complete sets of measures. This restricted the data set to 20 characters (Table 1) from 46 specimens (29 from Asia and 17 from Australia). A PCA was also run using the percentage condylobasal length for the skull measurements. This was undertaken to account for the potential confounding factor of size differences, given the generally greater condylobasal lengths of specimens from Australia.

A further PCA was run to assess geographical and habitat differences between specimens from Asia. The PCA was restricted to only those Asian specimens which had a complete set of measures and excluded all Australian samples. A total of 29 specimens from seven Asian countries (eight riverine, seven lacustrine and 14 marine) were analysed.

Additional univariate analyses were undertaken on characters highlighted by the multivariate analyses as causing a significant amount of variation within the dataset. This allowed analyses of a larger number of specimens (98 cranially mature specimens). All univariate analyses were undertaken using SPSS 9.1 (SPSS, 2001). We used Mann-Whitney tests at the 95% probability level. Comparisons of lengths for various characters were undertaken using one-tailed tests.

RESULTS

Geographic Variation Between Australia and Asia

The PCA clearly separated Australian specimens (the single PNG specimen was not included, because of too many missing variables) from all Asian specimens (Fig. 3), including the type specimen of *O. brevirostris* and one of the specimens Anderson (1879) used to characterise the osteology of *O. fluminalis*. The PCA reduced the original 20 measures to three principal components that together accounted for 76.14% of the variance (PCI 45.83%, PCII 24.48%, PCIII 5.83%) (Table 2).

On the first axis, Australian samples were characterised by, in decreasing order of importance: greater length of antorbital process, greater height of temporal fossa, greater length of rostrum, higher number of nasal bones/ossicles, greater separation between posterior margin of mesethmoid plate and anteriormost nasal bones/ossicles, greater length of temporal fossa and greater condylobasal length values, as well as lower minimum distance between pterygoid hamuli, smaller depth of pterygoid region and lower average width of nasal bones/ossicles.

The PCA was rerun using the percentage condylobasal length for all skull measurements. This resulted in the same clear separation between Australian and Asian specimens.

Standard Measures and Counts. – The univariate analyses showed highly significant differences (Mann-Whitney test, $p < 0.001$) for the following measurements between Australian and Asian specimens: condylobasal length ($n=94$, $U = 575.5$), rostrum length ($n=93$, $U = 255.0$), greatest width of premaxillary ($n=97$, $U = 515.0$), width of external nares ($n=98$, $U = 300.0$), length and height of temporal fossa ($n=95$,

$U = 246.0$; $n=94$, $U = 14.0$, respectively), length of orbit ($n=85$, $U=403.0$) and length of antorbital process ($n=90$, $U = 2.0$).

The Australian specimens generally had larger condylobasal lengths than Asian specimens ($306.4 \text{ mm} \pm \text{s.d. } 10.42$; $293.7 \text{ mm} \pm \text{s.d. } 15.58$, respectively, see Fig. 4). Australian specimens also had a greater rostrum length than Asian

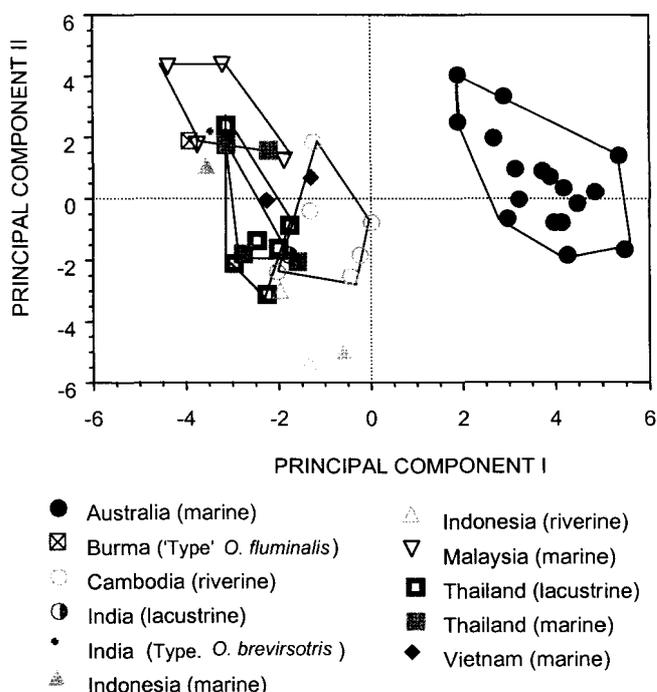


Fig. 3. Results from PCA for *Orcaella* skull characters, using a subset of specimens with no missing values. There is clear separation between Australian ($n=18$) and Asian specimens ($n=20$). Although Anderson (1879) donated numerous *O. fluminalis* specimens to various institutes, the designation and location of the 'type' specimen still needs to be confirmed.

Table 2. Eigenvectors from the PCA of Australian versus Asian specimens (Fig. 3a), based on a reduced dataset of specimens with no missing values (Appendix 1).

Measure	PCI	PCII	PCIII
Condylobasal length	0.2384	-0.2633	-0.0422
Length of rostrum	0.2652	-0.1241	-0.0305
Width of rostrum at base	0.2065	-0.2894	-0.1867
Width of rostrum at half length	0.2309	-0.1301	0.0430
Width premaxillary at half length	0.0746	-0.3832	0.2180
Greatest width of premaxillary	-0.0558	-0.3745	-0.0955
Postorbital width	0.2116	-0.2827	-0.1136
Zygomatic width	0.2079	-0.3048	-0.0805
External nares width	-0.1574	-0.3510	0.0806
Length of temporal fossa	0.2416	-0.1240	-0.0825
Height of temporal fossa	0.2788	0.1050	0.1997
Length of orbit	0.0578	-0.1702	0.6475
Length of antorbital process	0.2883	0.0533	0.0382
Mesethmoid plate separation	0.2712	0.1202	0.0382
Number of nasals	0.2521	0.1263	0.0121
Average length of nasals	-0.2140	-0.1574	-0.1864
Average width of nasals	-0.2633	-0.0703	-0.4395
Minimum pterygoid distance	-0.2778	-0.1601	-0.2574
Maximum pterygoid distance	-0.2501	-0.2257	0.1638
Depth of pterygoid region	-0.2560	-0.2100	0.0397

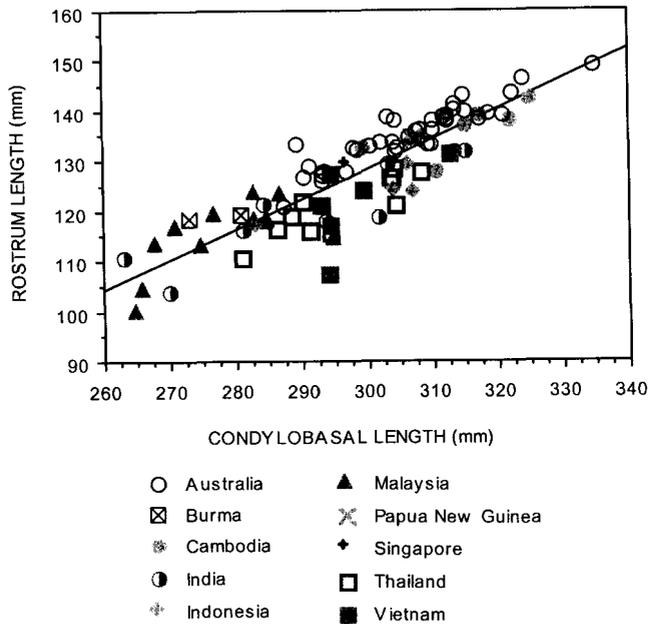


Fig. 4. Scatterplot of rostral length against condylobasal length, showing the linear relationship between these characters. The regression equation is: length of rostrum = $-63.33 + .64 \times$ condylobasal length; $R^2=0.793$. Note the generally larger condylobasal length of Australian specimens.

specimens ($135.4 \text{ mm} \pm \text{s.d. } 5.74$; $122.2 \text{ mm} \pm \text{s.d. } 9.34$, respectively). This is consistent with the direct relationship between rostral length and condylobasal length generally found in delphinids. Specimens were compared using rostrum length as a percentage of condylobasal length. This showed that the rostrum lengths of Australian specimens were proportionally greater than the specimens from Asia (mean = 44.2%, range 42.1 – 46.2%; versus, mean = 41.6%, range 36.5 – 44.6%, respectively).

Another character accounting for a significant amount of variation in the PCA was length of the antorbital process (Fig. 5a). In Australian specimens, the length ranged from 31.80 – 53.16 mm, compared with the Asian specimens, which ranged from 16.97 – 32.65 mm. A plot of antorbital process length versus condylobasal length (Fig. 5b) suggests that this is not just a correlate of the generally larger size of Australian specimens. For comparable condylobasal lengths, the Australian specimens had a greater antorbital length, with the Australian samples clustering above the regression line.

The height of the temporal fossa was also significantly greater in the Australian specimens (Figs. 6 and 7). Temporal fossa heights ranged from 49.10 – 83.20 mm, compared to 33.00 – 55.26 mm for Asian specimens.

There were also significant differences (Mann-Whitney test, $p < 0.05$) between the two regions in width of rostrum at the base ($n=94$, $U = 679.5$), width of rostrum at half length ($n=91$, $U = 562.0$), and preorbital width ($n=96$, $U = 821.0$).

Both upper and lower tooth/alveoli counts varied significantly between geographic regions. Tooth counts ranged from 8-19/11-18 in Asian specimens and 16-22/14-

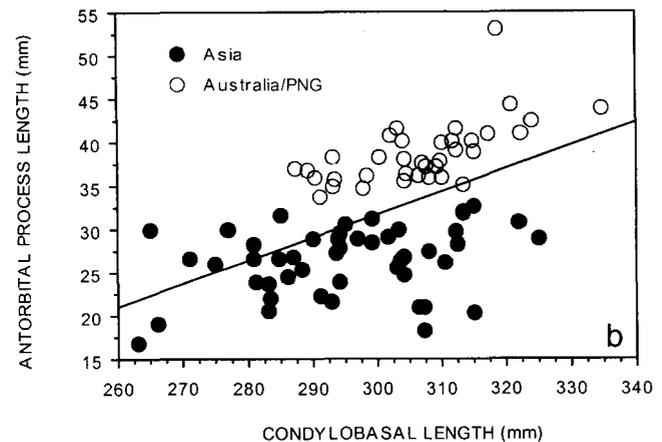
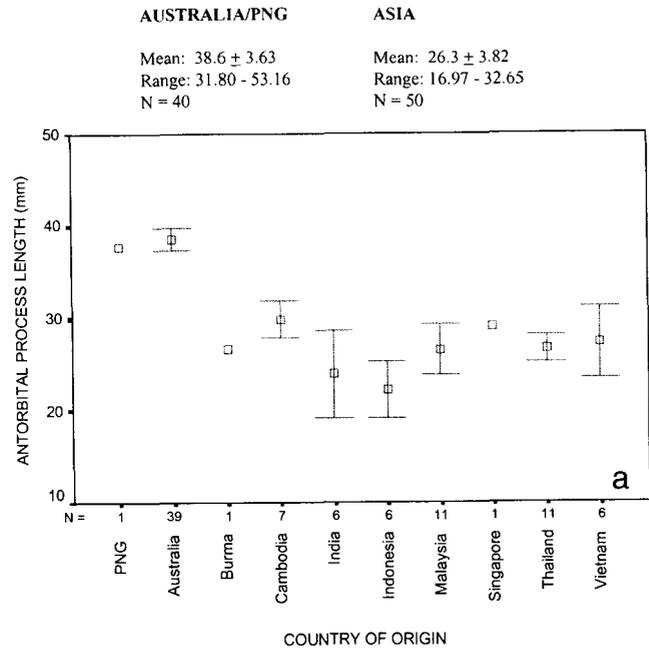


Fig. 5. Variation in length of antorbital process between countries, showing means and 95% confidence intervals. Mean, standard deviation and range are given for specimens from Australia/PNG and the combined Asian countries (a). Scatterplot of the length of antorbital process against condylobasal length. The regression equation is: length of antorbital process = $-49.93 + .275 \times$ condylobasal length; $R^2=0.361$ (b).

19 in Australian specimens. Due to a number of missing values, only the greatest upper and lower tooth counts were included in the univariate analyses. There was a highly significant difference between the two regions in both greatest upper ($n=77$, $U = 124.0$) and lower ($n=56$, $U = 32.5$) tooth/alveoli counts (Mann-Whitney test, $p < 0.001$).

Additional Measurements. – Nasal Bones/Ossicles. As a result of Australian specimens generally having a greater number of nasal bones/ossicles than Asian specimens, the average nasal length and width of individual specimens were analysed and included in the PCAs.

The number of nasal ossicles/depressions in Australian specimens ranged from 0-6, with a mean of 3.0 ± 1.77 . However, there appeared to be a second mode or peak at '0' ossicles/depressions (Fig. 8). In those cases scored '0', we

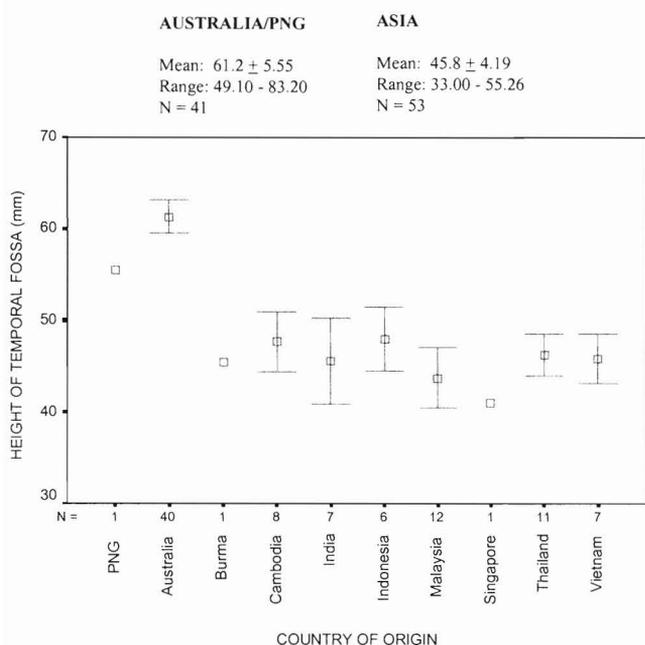


Fig. 6. Height of temporal fossa by country, showing means and 95% confidence intervals. Mean, standard deviation and range are given for specimens from Australia/PNG and the combined Asian countries.

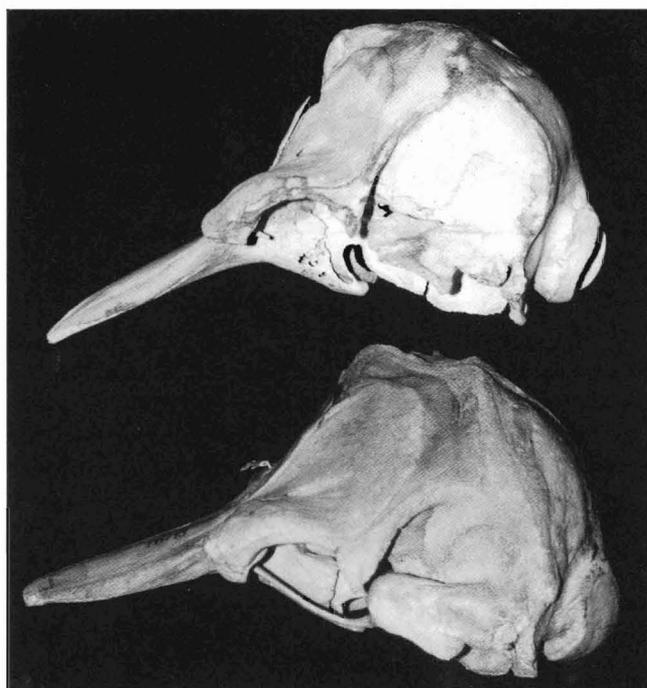


Fig. 7. Difference in temporal fossa height between a specimen from Australia (NMNH 284429, Appendix 1, 172) (above) and the Mahakam River, Indonesia, Asia (NMNH 199743, Appendix 1, 171) (below).

cannot be sure that nasal ossicles were in fact absent. In some skulls, the vertex appeared to be worn, in others there is the possibility that nasal ossicles had become fused with the underlying cranial bones. The ossicles ranged from 5.49 – 15.75 mm long by 5.06 – 13.97 mm wide. Average ossicle length and width/individual specimen ranged from 7.28 – 15.03 mm and 5.75 – 13.22 mm respectively (Fig. 9). The posteromedial nasal ossicles were located at the highest point

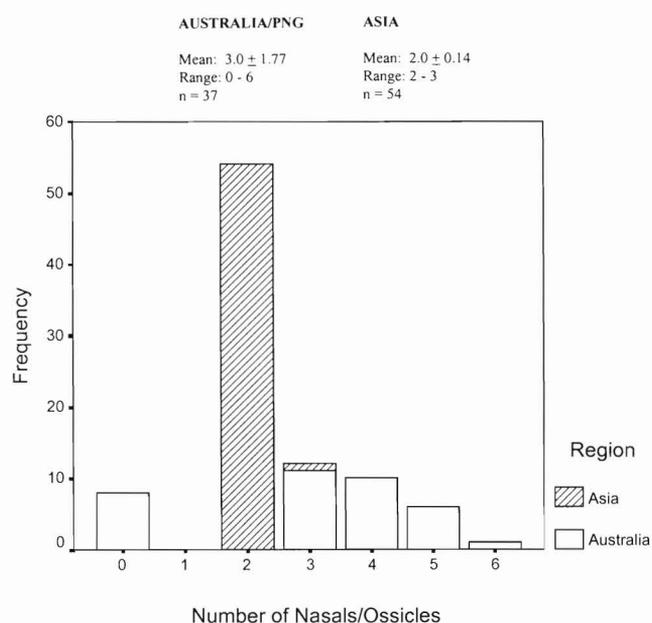


Fig. 8. Bar graph showing the number of nasal bones/ossicles for Asian and Australian specimens. One outlier (OBRE 03) from Malaysia was found to have three nasal depressions, whereas all other Asian specimens had two nasal bones/depressions. Mean, standard deviation and range are given for specimens from Australia and the combined Asian countries. The specimen from PNG was one of those which had no visible nasals and was scored as '0'.

of the vertex of the skull, while the lateral ossicles were situated anteriorly and lower on the face of the vertex, descending towards the mesethmoid plate (Fig. 10a).

In 54 of 55 Asian specimens, there were two nasal bones in the vertex (Fig. 8). The single exception was a skull from Malaysia (OBRE 03), which had three clear depressions in the vertex (see Discussion). The nasal bones/depressions were transversely elongate and oval-shaped, being antero-posteriorly compressed (Fig. 10b). They ran anteroventrally on either side of the vertex. Measurements ranged from 8.30 – 20.30 mm long by 9.51 – 22.96 mm wide. Average nasal length and width/individual specimen ranged from 10.40 – 18.84 mm and 10.50 – 21.08 mm, respectively.

There were highly significant differences between the two regions in average nasal length (Mann-Whitney test, $n=69$, $U = 78.0$, $p<0.001$) and average nasal width (Mann-Whitney test, $n=69$, $U = 26.0$, $p<0.001$). The average width of the nasal ossicles in Australian specimens was approximately half that in Asian specimens (Fig. 9).

Mesethmoid Plate. In 34 of the 35 Australian specimens measured, the mesethmoid plate was thin and poorly developed, leaving much of the frontal bone on the anterior face of the vertex exposed. Within this space, there was often a medially placed supernumerary bone (Fig. 10a; see also Arnold & Heinsohn, 1996). The most posterior part of this thin mesethmoid plate was usually lower on the face of the vertex than the anterior-most nasal ossicle/depression (Fig 2. – f), with a separation value of 0.92 – 12.26 mm. In specimen MM92, however, the posterior margin of the

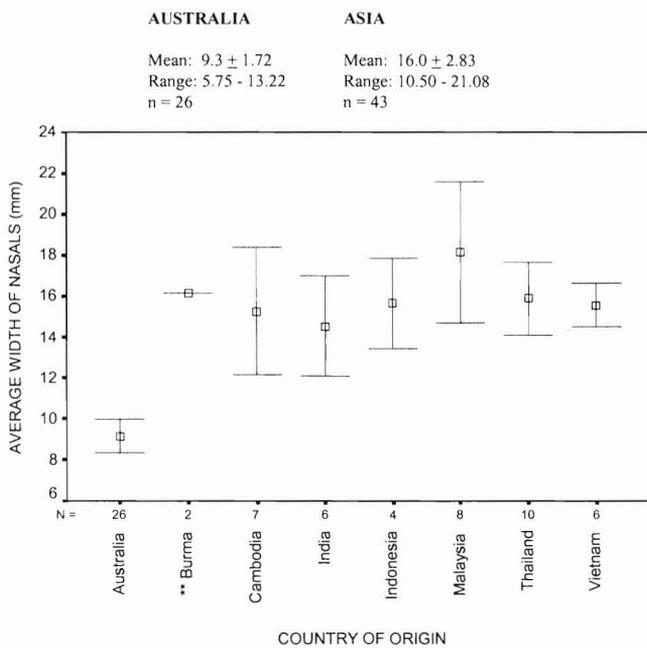


Fig. 9. Average width of nasal bones/ossicles by country, showing means and 95% confidence intervals. Only the mean is given for those countries with fewer than four specimens (indicated by asterisks). Mean, standard deviation and range are given for specimens from Australia and the combined Asian countries. The specimen from PNG was one of those which had no visible nasals and was not included in this analysis.

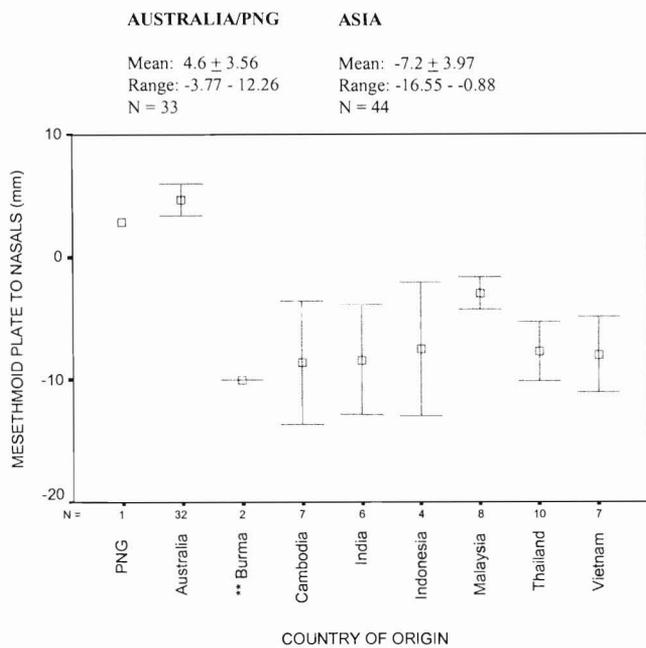


Fig. 11. Separation between posterior margin of mesethmoid plate and anteriormost point of nasal bone/ossicle by country, showing means and 95% confidence intervals. Specimens in which the mesethmoid plate extended posterior to the anteriormost point of the nasal bones/ossicles have a negative separation value. Only the mean is given for those countries with fewer than four specimens (indicated by asterisks). Mean, standard deviation and range are given for specimens from Australia/PNG and the combined Asian countries.

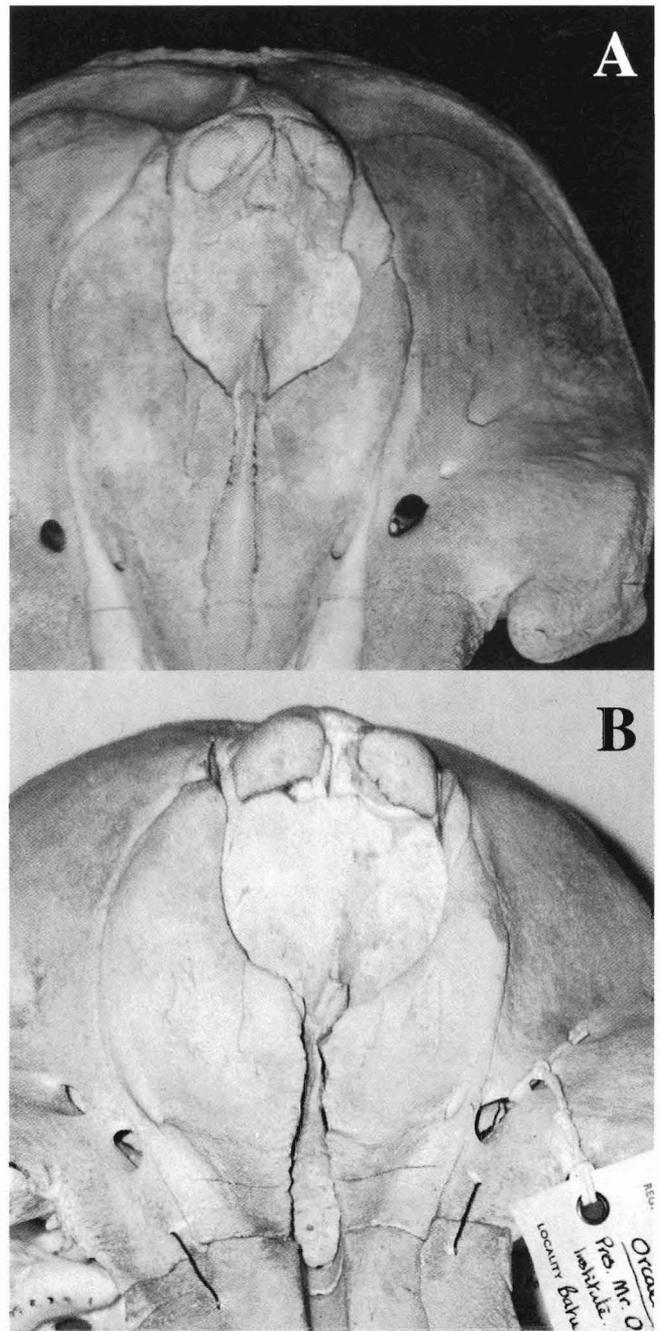


Fig. 10. Illustration of the vertex region of *Orcaella* in a specimen from Australia (QMJM4740, MM1013, Appendix 1, 126) (a) and Malaysia, Asia (BMNH 1964.2.24.1, Appendix 1, 73) (b). Note the larger number and smaller widths of nasal ossicles, the reduced mesethmoid plate and exposed frontal bone (with supernumerary bone) on the vertex of the Australian specimen.

mesethmoid was higher than the antero-most nasal ossicle/depression, giving a separation value of -3.77 mm (Fig. 11).

In all specimens from Asia, the mesethmoid plate was thick and well developed, normally close to or even in contact with the nasal bones (Fig. 10b). In all specimens in which this feature could be measured, the mesethmoid plate almost completely covered the anterior face of the vertex, with its posterior margin higher on the anterior face than the antero-most point of the nasal bones (hence with a negative separation value). Separation values ranged from -16.55 to -0.88 (Fig. 11).

There was a highly significant difference between Australian and Asian specimens in the separation between the mesethmoid plate and the nasal bones/ossicles (Mann-Whitney test, $n=77$, $U = 9.0$, $p<0.001$).

Pterygoid Hamuli. In specimens from Australia, the pterygoid hamuli had medial flanges, and the minimum distance between the medial flanges was consistently small (Fig. 12a). Minimum separation ranged from 1.56 – 9.81 mm (Fig. 13), while maximum separation ranged from 8.73

– 20.22 mm. The depth of the pterygoid hamuli in Australian specimens was consistently smaller than the Asian specimens and ranged from 19.43 – 31.20 mm (Fig. 14).

In all Asian specimens the pterygoid hamuli were widely separated (Fig. 12b), without any medial flanges. The minimum distance between the pterygoid hamuli ranged from 7.90 - 20.73 mm (Fig. 13), while maximum separation ranged from 11.00 – 24.32 mm. The depth of pterygoid hamuli ranged from 30.66 – 48.63 mm (Fig. 14).

There were highly significant differences (Mann-Whitney test, $p<0.001$) in minimum ($n=70$, $U = 3.0$) and maximum pterygoid distance ($n=70$, $U = 173.5$) and a greater depth of pterygoid region ($n=64$, $U = 1.5$) in Asian specimens.

A plot of minimum versus maximum pterygoid hamuli distances resulted in clear separation between the minimum distances of the two geographical areas, and partial separation between the maximum distances (Fig. 15a), although there is overlap with two specimens (one specimen, OBRE 03 from Malaysia and one specimen, MM92 from Australia). The pterygoid ratio (minimum distance / maximum distance x 100) ranged from 12.24 – 48.74 in Australian specimens and 48.53 – 100.00 in Asian specimens. A scatterplot of the pterygoid ratio versus the depth of pterygoid region resulted in very clear separation of Australian and Asian specimens (except for the consistent outlier OBRE 03, from Malaysia) (Fig. 15b).



Fig. 12. Illustration of the pterygoid region of *Orcaella* in an Australian specimen (QMJM4721, Appendix 1, 98) (a) and an Asian specimen from the Mekong River, Cambodia (CU2535 11-25, Appendix 1,18) (b). Note the medial flanges on the pterygoid hamuli of the Australian specimen, with narrower separation of the hamuli.

Variation with Habitat Between Australia and Asia

There are no known isolated freshwater populations of

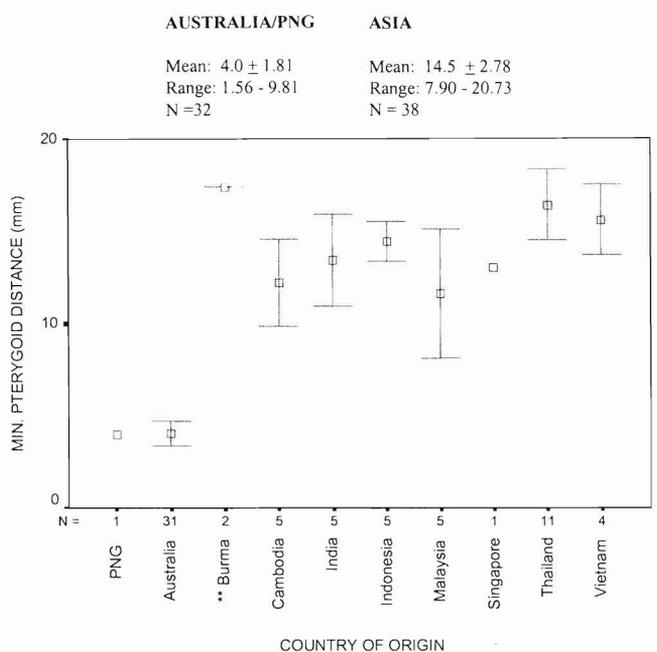


Fig. 13. Minimum separation of pterygoid hamuli by country, showing means and 95% confidence intervals. Only the mean is given for those countries with fewer than four specimens (indicated by asterisks). Mean, standard deviation and range are given for specimens from Australia/PNG and the combined Asian countries.

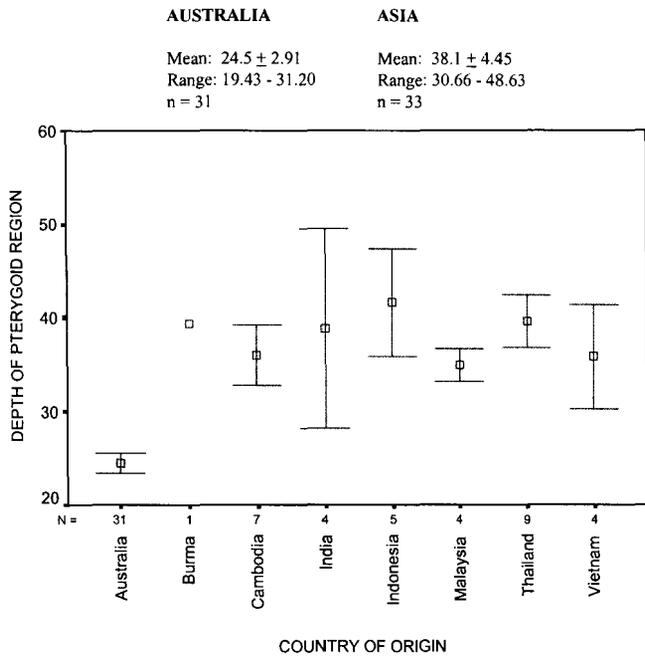


Fig. 14. Plot of depth of pterygoid region by country, showing means and 95% confidence intervals. Mean, standard deviation and range are given for specimens from Australia and the combined Asian countries. The specimen from PNG was excluded from this analysis due to incomplete measures.

Orcaella within Australia, and all of the specimens (including that in the Brisbane River) are considered marine. There was a clear separation of Australian specimens from Asian specimens, whether they were collected at marine or freshwater (riverine or lacustrine) sites (Fig. 3). The differences demonstrated here between Australian and Asian specimens can thus be attributed to geographical factors without the confounding effect of habitat.

Geographical and Habitat Variation Within Asia

The PCA was rerun on the dataset for Asian specimens only (Fig. 16). The PCA reduced the original 20 measures to three principal components that accounted for 62.88% of the variance (PCI 36.85%, PCII 14.84% and PCIII 11.19%). On the first axis, the primary factor responsible for potential variation was a greater width of the premaxillaries and greater width of rostrum at base, as well as lower mesethmoid plate and average width of nasal values (Table 3). The PCA suggests some geographical variation (Fig. 16). For example, there was minimal overlap between samples from Malaysia (marine) with those from Cambodia (riverine) or Thailand (marine and lacustrine).

There were also suggestions of separation by habitat. For example, there was no overlap between specimens from the Thailand lacustrine (Songkhla Lake) and Thailand marine sites. However, there was substantial overlap of the specimens from marine sites in Thailand with those from riverine sites (Cambodia) and lacustrine sites (India). Moreover, Anderson's specimen of *O. fluminalis* from the Ayeyarwady River clumped with the type of *O. brevirostris* (marine) near the Thailand lacustrine and Malaysian marine

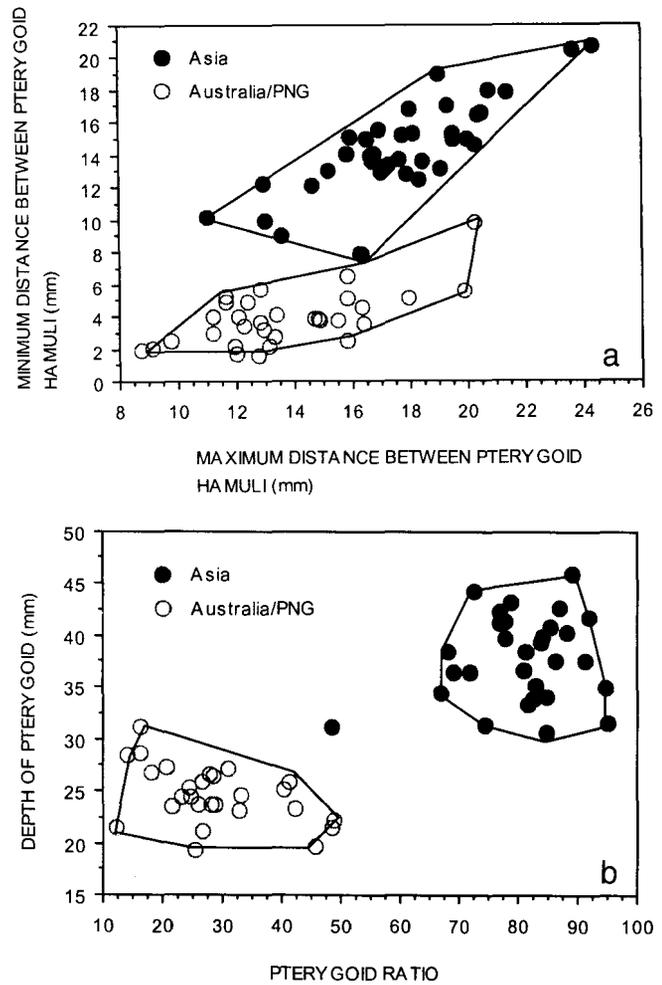


Fig. 15. Scatterplot of the minimum versus maximum distance between pterygoid hamuli according to region. There is no overlap, except for specimens OBRE 03 (Malaysia, Asia) and MM92 (Australia) (a). Scatterplot of depth of pterygoid region versus pterygoid ratio, according to region. The one outlier, as shown in this plot, is OBRE 03 from Malaysia (b).

specimens. Given the small sample sizes and the problem of potentially confounding effects between country and habitat, we do not consider such regional and habitat separations further.

DISCUSSION

Variation between Australia and Asia

Both univariate and multivariate analyses of skull characters suggest a clear separation of specimens from Australia (including one specimen from PNG) and Asia.

Standard Measures and Counts. – Pilleri & Gühr (1973-74: Table 9) gave dimensions for eight skulls from Asia. Included in these measures was the British Museum (Natural History) specimen from Singapore (BM 1888.11.20.2) which was described as having a percentage rostral length of 50% (much higher than the range calculated in this study for both Asian and Australian specimens). When the specimen was re-measured for this study, it was found that the condylobasal

length was similar (297 mm, this paper; 300 mm, Pilleri & Gahr, 1973-74); however, the rostrum length was found to be only 129 mm (versus the reported length of 150 mm). This resulted in a proportional rostrum length of 43.4%, which is within our range for Asian animals.

Additional Measures. – Asian specimens had the standard delphinid (and general mammalian) pattern of two nasal bones. Australian specimens generally had a larger number of nodular nasal bones/ossicles (mean 3.0 ± 1.77 , range 0-

6). There was overlap in the lengths of nasal bones of Asian specimens and nodular bones/ossicles of Australian specimens, whereas the width of the ossicles in Australian specimens was about half that of the nasal bones in Asian specimens. These nodules appear to represent multiple points of ossification, which remain uncoalesced in the Australian specimens. One skull from Malaysia (OBRE 03) had three nasal depressions. In two specimens from the Mekong River, collected near Kratie, Cambodia, each nasal bone was composed of two ‘osselets’, which were described as more or less fused (Lloze, 1973). Figures 14 and 17 from Lloze’s thesis, nonetheless, show that in both his specimens (ObKMC1 and ObKMC2) there are two nasal bones, with the presence of ‘osselets’ indicated by incomplete suture lines. Busnel et al. (1968) noted separate nasal ossicles in a specimen of striped dolphin *Stenella coeruleoalba* from the Mediterranean, and fused ossicles in another specimen of spinner dolphin *Stenella longirostris*. Thus, the presence of nasal ossicles is not restricted to Australian specimens of *Orcaella*, although their prevalence within that population does appear to be unique.

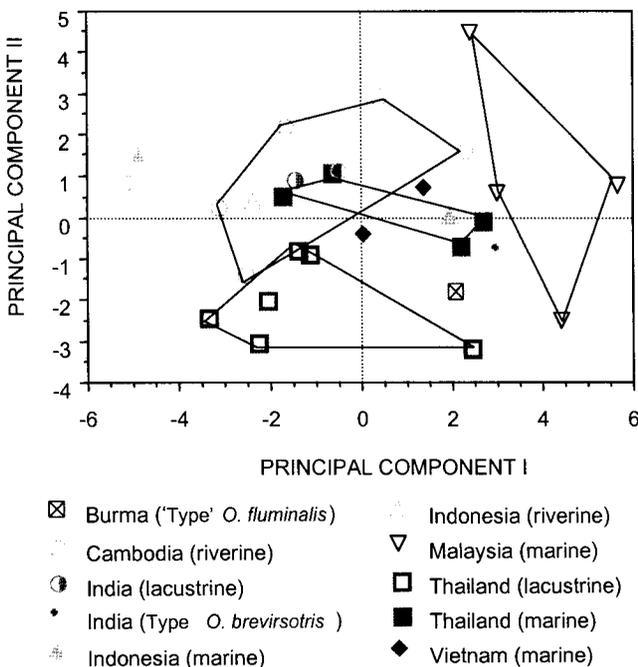


Fig. 16. Results from PCA using only Asian specimens with no missing values. This analysis included specimens from riverine (n=8), lacustrine (n=7) and marine (n=14) habitats. There are indications of possible further separations between geographic areas and habitat, however conclusions can not be reliably made, due to the small sample size.

There was a significant separation between the two geographic regions with regards to the minimum and maximum distance between the pterygoid hamuli. The Australian specimens consistently had medial flanges and a small ratio of maximum and minimum length between the pterygoid hamuli. This is compared to the Asian specimens, in which there was large separation between the pterygoid hamuli, which resulted in a large pterygoid ratio. This large separation of the pterygoid hamuli is also seen in Phocoenidae and Monodontidae (especially *Neophocaena phocaenoides* and *Delphinapterus leucas*), which have been previously shown to be outgroups to delphinids (de Muizon, 1988; Heyning, 1989; Gretarsdottir & Arnason, 1992). This may indicate that the large pterygoid separation shown by Asian specimens represents a more generalised condition,

Table 3. Eigenvectors from the PCA of Asian specimens (Fig. 16) based on a reduced data set with no missing values (Appendix 1).

Measure	PCI	PCII	PCIII
Condylobasal length	-0.2994	0.1347	0.2416
Length of rostrum	-0.2123	0.1005	0.2424
Width of rostrum at base	-0.3104	0.1635	-0.0392
Width of rostrum at half length	-0.2548	0.1078	-0.1145
Width premaxillary at half length	-0.3265	0.0437	-0.0229
Greatest width of premaxillary	-0.2566	0.1471	-0.3084
Postorbital width	-0.3096	0.1865	0.1120
Zygomatic width	-0.3176	0.1571	0.1180
External nares width	-0.2601	-0.1963	-0.1807
Length of temporal fossa	-0.2132	-0.2020	0.1702
Height of temporal fossa	-0.1346	-0.2375	0.2670
Length of orbit	-0.1769	0.0642	-0.2585
Length of antorbital process	-0.0491	-0.0028	0.5648
Mesethmoid plate separation	0.2496	0.0997	-0.0952
Number of nasals	0.0628	0.2813	0.1526
Average length of nasals	-0.1264	0.2627	-0.1868
Average width of nasals	0.0206	0.2998	-0.3128
Minimum pterygoid distance	-0.1022	-0.4837	-0.1239
Maximum pterygoid distance	-0.1362	-0.3912	-0.1309
Depth of pterygoid region	-0.2414	-0.2750	-0.1728

whereas the Australian specimens represents the more derived condition. The only exception in this case was shown by one Malaysian specimen (OBRE 03), which had a relatively low pterygoid ratio, similar to the upper limits of the Australian specimens.

The Australian specimens had thin, poorly-developed mesethmoid plates, in which much of the frontal bone on the anterior faces of the vertebrae were left exposed. In a few specimens, there was a posterior extension of the mesethmoid plate medially, but the plate was still markedly reduced and thinner at its edges. This contrasted with the condition in specimens from Asia, where the mesethmoid plate was thick and ran high onto the vertex, close to or contacting the nasal bones. De Muizon (1988) and Barnes (1990) considered a well-developed mesethmoid to be a diagnostic character of delphinids, suggesting it as the cause for both the apical position and transversely elongate form (through antero-posterior compression) of the nasal bones. This study (see also Arnold & Heinsohn, 1996) suggests that the development of the mesethmoid plate can vary intraspecifically.

As indicated by Arnold & Heinsohn (1996), both the form of the mesethmoid plate and the nasal bones in Australian specimens of *Orcaella* may represent retained juvenile features. However, as with the other characters of the vertex and possibly the pterygoid region, it is the Australian specimens that show the more derived or specialised condition.

Evolutionary Direction of Geographical Variation

Given the apparently more specialised characters in Australian specimens (especially those of the skull vertex), we suggest that they have been derived from the more generalised Asian populations. The presence of qualitative, as well as quantitative, morphological characters separating the Asian and Australian specimens, and the consistency of this separation (with a single specimen from Malaysia being the only apparent mismatch among 124 specimens examined), suggests that a major geographic/ecological barrier has operated for some time. The two major clusters of specimens (Fig. 3) correspond roughly to the Sunda and Sahul shelves respectively, which have maintained their separation even during periods of lowered sea levels in the Pleistocene Ice Ages (Woodland, 1983; Holloway & Hall, 1998; Randall, 1998). The intervening area of deep, oceanic water between the Sunda and Sahul shelves would have been a potential ecological barrier to an animal such as *Orcaella*, which appears to be closely associated with coastal/estuarine and riverine habitats (Stacey & Leatherwood, 1997; Stacey & Arnold, 1999). The closer juxtaposition of the Lesser Sunda Islands with the margin of the Sahul shelf during lower sea levels and the probable coastal habitats along the Sahul shelf margin at that time, may have provided a temporary

corridor for *Orcaella* to disperse from Asian to Australian waters.

Confirmed locality records of Irrawaddy dolphins (Stacey & Leatherwood, 1997) show two groupings, one to the west of Wallace's Line, through the Makassar Strait and one to the east of Lydekker's Line in western Papua New Guinea and throughout northern Australia. There is a single record from southwestern Sulawesi, indicating a crossing of Wallace's Line into Wallacea. There is no *a priori* reason to expect that Sulawesi and other areas within Wallacea have been less adequately examined for *Orcaella* than other Indonesian localities. However a better knowledge of the distribution of Irrawaddy dolphins within Indonesia and the variation in skull characters throughout the Indonesian Archipelago are necessary to suggest potential distribution barriers in this geologically complex area.

Variation Within Asian Countries

There were suggestions of separation by country and habitat. Given the limitations of our data set, we can only point out such apparent differences. Other techniques, such as genetic analysis, may provide more conclusive evidence of regional/habitat variation within Asia. Such studies are being carried out by K.M. Robertson (Southwest Fisheries Science Center, La Jolla, CA, USA).

CONCLUSIONS

The Principal Component Analyses clearly separated specimens from Australia, from specimens collected in marine, lacustrine and riverine sites throughout the Asian range of the species, including the type specimen of *O. brevirostris* and one of the specimens of '*O. fluminalis*' from Burma described by Anderson (1879).

This suggests that the large genetic differences shown by LeDuc et al. (1999) resulted from a major geographic separation corresponding to the classical Oriental/Australian zoogeographical realms, rather than habitat (marine/freshwater).

From the results of our analyses, the Australian specimens should be considered taxonomically distinct, at least as a subspecies, but possibly at the species level. We do not formally name the taxon here, but plan to address the systematics of *Orcaella* in the future, incorporating further osteological and morphological characters and taking into account parallel genetic studies.

Irrespective of eventual taxonomic decisions, our results suggest that a single site, e.g. northern Australia, cannot conserve the genetic diversity of Irrawaddy dolphins. An increased effort to identify and conserve populations within Asia should therefore be given high priority.

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Appendix 1. Details of Orcaella specimens examined.

SPECIMEN	PCA	REG. NO	TYPE	HABITAT	ORIGIN	COUNTRY	INSTITUTE	COUNTRY
4		ZRC. 4.7895	partial skull	marine	Singapore	Singapore	Zoological Reference Collection	Singapore
18	PCA	2535 11-25	skull	freshwater	Mekong River	Cambodia	Chulalongkorn University	Thailand
32	PCA	un-numbered	full skeleton	marine	Thailand	Thailand	Buarapa University	Thailand
46	PCA	73.13	skull	marine	Sarawak, Malaysia	Malaysia	Sarawak Museum	East Malaysia
47		73.14	skull	marine	Sarawak, Malaysia	Malaysia	Sarawak Museum	East Malaysia
48	PCA	73.15	skull	marine	Sarawak, Malaysia	Malaysia	Sarawak Museum	East Malaysia
65		PT/UPM/MM001	skull	marine	Pulau Libiran	Malaysia	Sabah Parks, Manukan Island	East Malaysia
66		SEL.01	skull	marine	Pulau Selinggaan	Malaysia	Turtle Island	East Malaysia
67		SEL.02	partial skull	marine	Pulau Selinggaan	Malaysia	Turtle Island	East Malaysia
69	PCA	un-numbered	full skeleton	freshwater	Mahakam River	Indonesia	Jaya Ancol Aquarium	Indonesia
72	PCA	ZD 1877.12.10.17	full skeleton	freshwater	Irrawaddy River, Burma	Burma	Natural History Museum	England
73		BM1964.2.24.1	skull	marine	Maung, Penang, Malaya	Malaysia	Natural History Museum	England
74		BM1888.5.28.1 (1454.d.)	skull	marine	Muara Is. Brunei, Borneo	Brunei	Natural History Museum	England
75		BM1883.11.20.2 (1454.c.)	skull	marine	Singapore	Singapore	Natural History Museum	England
76	PCA	BM1865.4.20.1 (1454.a.)	skull	marine	Harbour of Vizagapatam	India	Natural History Museum	England
77		563 (45751)	skull	lake	Songkla, Thale	Thailand	Stuttgard Museum	Germany
79	PCA	A-1199 (1877-454)	skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
80		A-1198	immature skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
81		1888-386 A	skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
82	PCA	1888 -386 B	skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
83		1888 - 389	skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
84		1888 - 388	skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
85		ZMA 5070	skull	freshwater	Long Eram, Midden, Mahakam	Kalimantan	Amsterdam Museum	Netherlands
86		ZMA 5071	skull	lake	Chilka, Lake Orissa	India	Amsterdam Museum	Netherlands
88		73.16	partial skull	marine	Kuching	Malaysia	Sarawak Museum	Malaysia
100		99610	immature skull	marine	Sarawak, Malaysia	Malaysia	Field Museum of Natural History	Chicago, USA
101		99613	skull	marine	Sarawak, Malaysia	Malaysia	Field Museum of Natural History	Chicago, USA
102		un-numbered	photo	marine	Bangladesh	Bangladesh	Dhakka Museum	Bangladesh
103		OBRE 01	skull	marine	Niah	Malaysia	University Malaysia Sarawak	East Malaysia
104		OBRE 02	skull	marine	Bako	Malaysia	University Malaysia Sarawak	East Malaysia
105	PCA	OBRE 03	skull	marine	Buntal	Malaysia	University Malaysia Sarawak	East Malaysia
135		un-numbered	partial skull	lake	Songkhla Lake	Thailand	National Institute of Coastal Aquaculture	Thailand
136	PCA	un-numbered	skull	lake	Songkhla Lake	Thailand	National Institute of Coastal Aquaculture	Thailand
137		un-numbered	partial skull	lake	Songkhla Lake	Thailand	Hat Yai University	Thailand
138	PCA	LFS 01	skull	lake	Songkhla Lake	Thailand	Lam Pam Fisheries Station	Thailand
139	PCA	LFS 02	skull	lake	Songkhla Lake	Thailand	Lam Pam Fisheries Station	Thailand
142	PCA	LFS 05	full skeleton	lake	Songkhla Lake	Thailand	Lam Pam Fisheries Station	Thailand
143	PCA	LFS 06	full skeleton	lake	Songkhla Lake	Thailand	Lam Pam Fisheries Station	Thailand
144	PCA	END 062	full skeleton	marine	Suratthani	Thailand	Phuket Marine Biological Station	Thailand
145	PCA	END 022	full skeleton	marine	Sumut Sungkram	Thailand	Phuket Marine Biological Station	Thailand
146		un-numbered	partial skull	marine	Mekong River Delta	Vietnam	Den Thang Nhi Temple	Vietnam
147		OBRE 01	partial skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
148	PCA	OBRE 02	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam

Appendix 1. (Continue)

SPECIMEN	PCA	REG. NO	TYPE	HABITAT	ORIGIN	COUNTRY	INSTITUTE	COUNTRY
149	PCA	OBRE 03	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
150		OBRE 04	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
151		OBRE 05	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
152		OBRE 06	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
153		OBRE 07	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
154		OBRE 08	skull	marine	Mekong River Delta	Vietnam	Dinh Thang Tam Temple	Vietnam
155			photo	marine	Mekong River Delta	Vietnam	Den Thang Nhat Temple	Vietnam
156			photo	marine	Mekong River Delta	Vietnam	Den Thang Nhat Temple	Vietnam
157			photo	marine	Mekong River Delta	Vietnam	Den Thang Nhat Temple	Vietnam
158			photo	marine	Mekong River Delta	Vietnam	Den Thang Nhat Temple	Vietnam
159			photo	marine	Mekong River Delta	Vietnam	Den Thang Nhat Temple	Vietnam
160			photo	marine	Mekong River Delta	Vietnam	Den Thang Nhat Temple	Vietnam
161	PCA	un-numbered	full skeleton	marine	Burapa Beach	Thailand	Buarapa University	Thailand
162		ZSI 13030	skull	freshwater	Irrawaddy River, Burma	Burma	Zoological Survey India	India
163		ZSI 274 ASB (19382)	skull	marine	Calcutta Fish Bazaar	India	Zoological Survey India	India
164		ZSI 2893 (19122)	skull	marine	Calcutta Fish Bazaar	India	Zoological Survey India	India
165		ZSI 19123	skull	marine	Circular Canal, Calcutta	India	Zoological Survey India	India
166	PCA	ZSI 19379	skull	lake	Chilka Lake	India	Zoological Survey India	India
169		1884-148	immature skull	freshwater	Mekong River	Cambodia	Mus. nat. d'Hist. naturelle	France
170	PCA	1880-18	skull	marine	near Hughli River	India	Mus. nat. d'Hist. naturelle	France
171	PCA	USNM199743 (1914.05)	skull	freshwater	Mahakam River	Indonesia	Smithsonian Institution	Washington, USA
174	PCA	21929	skull	marine	Sarawak, Malaysia	Malaysia	Museum of Comparative Zoology	Boston, USA
187		486170	partial skull	marine	Sumatra	Indonesia	Smithsonian Institution	Washington, USA
176		un-numbered	skull	lake	Chilka Lake	India	Bulgan Wildlife Department	India
177		un-numbered	partial skull	lake	Chilka Lake	India	Chilka Lake Management Authority	India
178		un-numbered	partial skull	lake	Chilka Lake	India	Bulgan Wildlife Department	India
179		un-numbered	skull	marine	Cheribon, Java	Indonesia	Balai Penelitian dan Pengembangan Zoologi - LIPI	Indonesia
180	PCA	un-numbered	skull	marine	Cheribon, Java	Indonesia	Balai Penelitian dan Pengembangan Zoologi - LIPI	Indonesia
181	PCA	13643	skull	marine	Keplauan, Scribu	Indonesia	Balai Penelitian dan Pengembangan Zoologi - LIPI	Indonesia
182	PCA	OBRE01-18/04	skull	lake	Songkhla Lake	Thailand	Lam Pam Fisheries Station	Thailand
183		CDF01	partial skull	freshwater	Stung Treng, Mekong River	Cambodia	Wildlife Conservation Society	Cambodia
184	PCA	CDF02	skull	freshwater	Tbong Klar, Mekong River	Cambodia	Wildlife Conservation Society	Cambodia
185	PCA	CDF03	skull	freshwater	Kratie, Mekong River	Cambodia	Department of Fisheries	Cambodia
186		CDF04	immature skull	freshwater	Kampi, Mekong River	Cambodia	Wildlife Conservation Society	Cambodia
94		JM4708 MM021	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
95		JM4700 MM06	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
96		JM4714 MM032	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
97		JM4720 MM54	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
98		JM4721 MM61	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
106		M33213	skull	marine	Daru	Papua New Guinea	Australian Museum	Australia
107		JM11976	partial	marine	Brisbane River	Australia	Queensland Museum	Australia
108		U0249	skull	marine	Northern Territory	Australia	Northern Territory Museum	Australia
109		U0532	skull	marine	Northern Territory	Australia	Northern Territory Museum	Australia

Appendix 1. (Continue)

SPECIMEN	PCA	REG. NO	TYPE	HABITAT	ORIGIN	COUNTRY	INSTITUTE	COUNTRY
110		U5079	skull	marine	Northern Territory	Australia	Northern Territory Museum	Australia
111		M23242 B1823	partial	marine	Western Australia	Australia	Western Australian Museum	Australia
112		M23243 B1824	skull	marine	Western Australia	Australia	Western Australian Museum	Australia
113	PCA	JM4704 MM12	skull	marine	Horseshoe Bay, Magnetic Island	Australia	Museum of Tropical Queensland	Australia
114		JM4705 MM13	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
115		JM4705 MM13A	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
116	PCA	JM4706 MM14	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
117		JM4706 MM14A	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
118	PCA	JM4751 MM024	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
119	PCA	JM4709 MM025	skull	marine	Horseshoe Bay, Magnetic Island	Australia	Museum of Tropical Queensland	Australia
120	PCA	JM4712 MM030	skull	marine	Pallarenda	Australia	Museum of Tropical Queensland	Australia
121	PCA	JM4725 MM81	skull	marine	Pallarenda	Australia	Museum of Tropical Queensland	Australia
122	PCA	JM4726 MM82	skull	marine	3 Mile Creek, Townsville	Australia	Museum of Tropical Queensland	Australia
123		JM4727 MM88	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
124	PCA	MM92	skull	marine	Kissing Point, Townsville	Australia	Museum of Tropical Queensland	Australia
126	PCA	JM4740 MM1013	skull	marine	Horseshoe Bay, Magnetic Island	Australia	Museum of Tropical Queensland	Australia
127		JM4752 MM1025	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
128		MM1039	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
129		JM4740 MMA	partial	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
130	PCA	JM4734 CET1003	skull	marine	Town common, Townsville	Australia	Museum of Tropical Queensland	Australia
131		JM4735 MMCET1005	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
132		unknown	skull	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
133		unknown	full skeleton	marine	Townsville	Australia	Museum of Tropical Queensland	Australia
134		JCU 1016	skull	marine	Townsville	Australia	James Cook University	Australia
135	PCA	JCU	skull	marine	Townsville	Australia	James Cook University	Australia
136	PCA	JCU 1026	skull	marine	Townsville	Australia	James Cook University	Australia
137	PCA	JM4736 CET1006	skull	marine	Townsville	Australia	James Cook University	Australia
138		JCU	skull	marine	Townsville	Australia	James Cook University	Australia
139		JCU 1032	skull	marine	Townsville	Australia	James Cook University	Australia
140		JM4707 MM6	skull	marine	Townsville	Australia	James Cook University	Australia
141		JCU	partial	marine	Townsville	Australia	James Cook University	Australia
142		JCU 1000	skull	marine	Townsville	Australia	James Cook University	Australia
143	PCA	JM 4748 JCU 1021	skull	marine	Townsville	Australia	James Cook University	Australia
144	PCA	JCU	skull	marine	Townsville	Australia	James Cook University	Australia
145	PCA	JCU	skull	marine	Townsville	Australia	James Cook University	Australia
172		USNM284429	skull	marine	Melville Bay, Northern Territory	Australia	Smithsonian Institution	Washington, USA
173	PCA	USNM284430	skull	marine	Melville Bay, Northern Territory	Australia	Smithsonian Institution	Washington, USA
175		5321	skull	marine	unknown location	Australia	Museum of Comparative Zoology	Boston, USA

Appendix 2: Descriptive statistics of *Orcaella* cranial measurements.

Standard Measures		Asia	Australia
Condylbasal length	**	n = 53 mean: 293.7 ± 15.58 range: 263.10 – 325.10	n = 41 mean: 306.4 ± 10.42 range: 287.20 – 334.80
Rostrum length	**	n = 53 mean: 122.2 ± 9.34 range: 100.00 – 142.52	n = 40 mean: 135.4 ± 5.74 range: 120.86 – 149.00
Width rostrum at base	*	n = 52 mean: 108.5 ± 7.53 range: 93.62 – 124.70	n = 42 mean: 113.6 ± 6.61 range: 99.29 – 125.60
Width rostrum 1/2 length	*	n = 51 mean: 65.3 ± 5.85 range: 49.00 – 77.32	n = 40 mean: 69.2 ± 3.57 range: 61.52 – 78.00
Width rostrum 3/4 length	*	n = 49 mean: 42.2 ± 6.13 range: 24.00 – 55.55	n = 39 mean: 45.8 ± 3.42 range: 34.82 – 51.65
Width premax 1/2 length	ns	n = 51 mean: 43.8 ± 4.50 range: 35.50 – 51.80	n = 40 mean: 42.4 ± 3.53 range: 32.00 – 49.52
Greatest width premax	**	n = 54 mean: 82.9 ± 4.17 range: 73.79 – 93.62	n = 43 mean: 78.33 ± 4.34 range: 66.87 – 86.30
Preorbital width	*	n = 54 mean: 173.8 ± 9.80 range: 152.30 – 196.00	n = 42 mean: 178.3 ± 6.92 range: 161.12 – 190.10
Postorbital width	ns	n = 55 mean: 200.4 ± 11.16 range: 172.10 – 219.20	n = 42 mean: 203.23 ± 7.41 range: 187.10 – 214.50
Zygomatic width	ns	n = 54 mean: 200.1 ± 10.57 range: 171.00 – 217.60	n = 43 mean: 203.1 ± 7.47 range: 187.2 – 215.00
External nares width	**	n = 55 mean: 45.8 ± 2.32 range: 40.70 – 50.08	n = 43 mean: 42.1 ± 2.29 range: 36.14 – 46.81
Internal nares width	ns	n = 41 mean: 54.2 ± 3.43 range: 47.14 – 63.00	n = 39 mean: 53.8 ± 1.77 range: 48.50 – 57.95
Temporal fossa length	**	n = 53 mean: 81.0 ± 7.41 range: 65.00 – 100.83	n = 42 mean: 92.6 ± 7.99 range: 84.15 – 112.35
Temporal fossa height	**	n = 53 mean: 45.8 ± 4.19 range: 33.00 – 55.26	n = 41 mean: 61.2 ± 5.55 range: 49.10 – 83.20
Length of orbit	**	n = 53 mean: 52.3 ± 2.36 range: 46.92 – 57.32	n = 32 mean: 54.6 ± 2.35 range: 49.99 – 58.20
Length of antorbital process	**	n = 50 mean: 26.3 ± 3.82 range: 16.97 – 32.65	n = 40 mean: 38.6 ± 3.63 range: 31.80 – 53.16
Length of upper toothrow	del.	n = 47 mean: 92.2 ± 12.83 range: 61.37 – 113.98	n = 39 mean: 106.7 ± 6.48 range: 92.69 – 122.85
Length of mandible ↘	del.	n = 29 mean: 228.0 ± 17.10 range: 199.40 – 290.00	n = 34 mean: 239.0 ± 10.08 range: 219.10 – 272.00

Appendix 2 (Continue)

Standard Measures		Asia	Australia
Height of mandible	del.	n = 29 mean: 70.3 ± 5.23 range: 58.00 – 77.45	n = 31 mean: 73.9 ± 3.28 range: 67.80 – 79.10
Tooth count: UR	**	n = 41 mean: 15.0 ± 1.90 range: 9 - 18	n = 35 mean: 18.3 ± 1.12 range: 16 – 20
Tooth count: UL	**	n = 40 mean: 15.2 ± 2.15 range: 8 - 19	n = 36 mean: 18.00 ± 1.82 range: 11 – 22
Tooth count: LR	**	n = 24 mean: 13.5 ± 1.69 range: 11 - 18	n = 31 mean: 16.8 ± 0.97 range: 14 – 18
Tooth count: LL	**	n = 25 mean: 13.8 ± 1.36 range: 11 - 17	n = 31 mean: 17.3 ± 0.90 range: 15 - 19
Mesethmoid plate	**	n = 44 mean: -7.2 ± 3.97 range: -16.55 – -0.88	n = 33 mean: 4.6 ± 3.56 range: -3.77 – 12.26
Number of nasals	**	n = 54 mean: 2.0 ± 0.14 range: 2 – 3	n = 37 mean: 3.0 ± 1.77 range: 0 - 6
Minimum pterygoid distance	**	n = 38 mean: 14.5 ± 2.78 range: 7.90 – 20.73	n = 32 mean: 4.0 ± 1.81 range: 1.56 – 9.81
Maximum pterygoid distance	**	n = 38 mean: 17.7 ± 2.75 range: 11.00 – 24.32	n = 32 mean: 13.7 ± 2.77 range: 8.73 – 20.22
Depth of pterygoid egion	**	n = 33 mean: 38.1 ± 4.45 range: 30.66 – 48.63	n = 31 mean: 24.5 ± 2.91 range: 19.43 – 31.20
Average nasal length	**	n = 43 mean: 14.3 ± 2.30 range: 10.40 – 18.84	n = 26 mean: 10.0 ± 1.74 range: 7.28 – 15.03
Average nasal width	**	n = 43 mean: 16.0 ± 2.83 range: 10.50 – 21.08	n = 26 mean: 9.3 ± 1.72 range: 5.75 – 13.22

‘***’ represents a highly significant difference (Mann-Whitney test, P<0.001)

‘**’ represents a significant difference (Mann-Whitney test, P<0.05)

‘ns’ represents no significant difference (Mann-Whitney test, P>0.05), and

‘del’ indicates that the character was not analysed due to many missing variables

± = standard deviation