

DESCRIPTION OF A NEW DOLPHIN,  
THE AUSTRALIAN SNUBFIN DOLPHIN  
*ORCAELLA HEINSOHNI* SP. N.  
(CETACEA, DELPHINIDAE)

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ABSTRACT

Comparisons of the Irrawaddy dolphin, *Orcaella brevirostris*, between Australian and Asian sites documented geographic differences in height of dorsal fin, presence or absence of a median dorsal groove in front of the dorsal fin, and coloration (presence or absence of a dorsal cape). Analysis of genetic data provided support for two clades within the Asian samples, the Mekong River samples from Cambodia and southern Laos, and all other marine and freshwater sites from Thailand, Indonesia, and the Philippines. The major separation, however, was between sites in Asia and those from Australia (5.9% of base pair differences, compared with 1.2% for within Australia and 1.5% for within Asia). Within a 403 base segment of the mtDNA control region, Australian specimens had 17 diagnostic sites with 16 fixed base pair differences and one insertion/deletion. Consistent, statistically significant differences in skull characters of Australian specimens have previously been demonstrated and are reviewed in this paper. There was a high concordance in character differences demonstrated between *O. brevirostris* from all Asian sites and Australian specimens, especially in the genetic and osteological characters. Based on the range and concordance of character differences, we propose that the Australian dolphins be recognized as a new species, *Orcaella heinsobni* (suggested common name: Australian snubfin dolphin).

Key words: Irrawaddy dolphin, snubfin dolphin, *Orcaella brevirostris*, *Orcaella heinsobni*, taxonomy, skull morphology, geographic variation, molecular analyses, external morphometrics.

*Orcaella brevirostris* (Owen in Gray 1866), the Irrawaddy dolphin, has been recorded from a wide range of coastal and riverine habitats from the northwestern Bay of Bengal to the east coast of Australia (Stacey and Leatherwood 1997). A small population occurring in Malampaya Sound, southern Philippines, was only recently documented (Dolar *et al.* 2002, Smith *et al.* 2004), and distribution throughout the species range is still incompletely known. Although the first *Orcaella* specimens from Australia were collected in 1948, their occurrence was only documented in the 1960s (Johnson 1964, Mörzer Bruyns 1966) with scattered records subsequently (Dawbin 1972, who also recorded *Orcaella* from Papua New Guinea; Marsh *et al.* 1989; Whiting 1997; Paterson *et al.* 1998; Chatto and Warnecke 2000). Parra *et al.* (2002) collated Australian records from museum specimens, aerial surveys, and unpublished reports.

*Orcaella* has recently received attention as one of the facultative freshwater cetaceans of Asia (Smith and Jefferson 2002) which, through its preference for riverine and coastal habitats, is subject to increasing human-induced threats. Consequently, the species requires increased conservation management (Perrin *et al.* 1996, Reeves *et al.* 2003a, b). Recent abundance estimates of particular populations, *e.g.*, in the Mahakam River of East Kalimantan, Indonesia (Kreb 1999, 2002); Songkhla Lake, Thailand (Beasley *et al.* 2002b); Malampaya Sound, Philippines (Smith *et al.* 2004); and Mekong River of southern Laos, Cambodia, and Vietnam (Smith and Beasley 2004a), number in the tens of animals. IUCN (the World Conservation Union) has listed several isolated subpopulations of *Orcaella* as “Critically Endangered”—the Mahakam River subpopulation listed in the 2000 Red List (Kreb and Smith 2000) and the Ayeyarwady River, Malampaya Sound, Mekong River, and Songkhla Lake subpopulations listed in the 2004 Red List (Smith 2004; Smith and Beasley 2004a, b, c). Thus, there is significant concern for the conservation of *Orcaella* throughout much of its range, particularly within Asia (Smith *et al.* 2003).

Smith and Jefferson (2002) noted that there are probably numerous populations of Irrawaddy dolphins and called for a clarification of taxonomic and demographic relationships throughout the range of the species. Based on examination of 124 *Orcaella* skulls from throughout their range, Beasley *et al.* (2002a) demonstrated that differences in cranial morphology existed between *Orcaella* from Australian (including one specimen from Papua New Guinea) and Asian sites. They suggested that the differences warranted taxonomic separation of the Australian populations at the subspecific or even specific level.

In this paper we extend the observations in Arnold and Heinsohn (1996) on external morphometrics and color pattern, based on a larger number of Asian specimens. We present new data on the genetic variation within and between populations from Asia and Australia. Incorporating this new information with a review of cranial anatomy (Beasley *et al.* 2002a) and postcranial osteology (Arnold and Heinsohn 1996), we redescribe and diagnose the Australian specimens, which we propose as a new species, *Orcaella heinsohni*.

## METHODS

### *External Morphometrics*

*Material and data collection*—External morphometrics were available for 26 Australian specimens (22 specimens from Arnold and Heinsohn 1996: table 6; plus four specimens: this paper, Appendix 1) and 34 Asian specimens (11 specimens from Arnold and Heinsohn 1996: table 7; plus 23 specimens: this

paper, Appendix 1). External measurements were taken according to Norris (1961). The specimens from Asia were measured separately by a number of researchers, either obtained through published and unpublished literature, or measured by the first author. In cases where the basis for measurements was unclear, data were excluded from the analysis. As body proportions of juvenile cetaceans may differ significantly from adults (Sergeant 1962), individuals less than 160 cm in length were excluded from the analysis. The exclusion of these specimens was based on limited data from Marsh *et al.* (1989) and preliminary principal component analyses (PCA), where specimens less than 160 cm formed a distinct cluster based on proportional size differences. Such exclusions reduced the data set to 22 Australian specimens and 20 Asian specimens (indicated by asterisk "\*" and "\*\*", respectively in Appendix 1).

Descriptive statistics were calculated for 17 measurements from these 42 specimens. However, sample size varied for the 17 measurements, due to inconsistencies in measurements. Two measurements were excluded for reasons of inconsistent measurement methods (dorsal fin height of 7.03% in Anderson (1879) (Appendix 1: Asia 49), was probably an oblique measurement (Lloze 1973, Arnold and Heinsohn 1996), and for one Cambodian specimen (Appendix 1: Asia 41) the tip of upper jaw to dorsal fin measurement was taken to the anterior of the fin rather than the fin tip). A further three measurements were clear outliers in the data set and also excluded (the value of 38.2% for tip of upper jaw to flipper as a percentage of total body length [Arnold and Heinsohn 1996: table 7, specimen 11] which was indirectly calculated and both the upper jaw to gape and upper jaw to eye measurements for one Australian specimen [Appendix 1: Australia 6]).

Due to such inconsistencies in measurements, as well as the state of decomposition in other specimens, eight measurements with a large number of missing variables were excluded from the multivariate analysis. The nine measurements remaining were: tip of upper jaw to gape, tip of upper jaw to blowhole, tip of upper jaw to dorsal fin, tip of upper jaw to flipper, anterior margin of flipper, maximum flipper width, dorsal fin height, dorsal fin length, and maximum width of tail.

Descriptive statistics and analyses were run on both absolute values and proportions, as a function of total length. Only the latter are presented here to better reflect shape, rather than size variation.

*Data analyses*—Descriptive statistics were used to examine the external morphometric variables and to test for significance using Mann-Whitney *U* tests. Nine proportional measurements from a reduced data set with no missing values (13 Australian and nine Asian specimens) were then compared using multivariate analyses (indicated by "\*" in Appendix 1). Multivariate analyses consisted of principal component analyses (PCA) and stepwise discriminant function analyses (DFA). Although sample size for multivariate analysis is significantly smaller than the full data set, it was considered preferable and more reliable to use actual data, rather than substitute means for missing values. The computer program SPSS 11 (SPSS 2003) was used for all univariate and DFA analyses and PC-ORD (McCune and Mefford 1999) for all PCA.

#### *Coloration*

The first author observed free-living and captive Asian *Orcaella* in Cambodia (riverine and coastal habitats), India (lacustrine), Indonesia (riverine), east and west

Malaysia (coastal), Philippines (coastal), and Thailand (lacustrine and coastal). Information on Australian specimens is from published photographs (see Appendix 6: *O. heinsobni*), unpublished photographs, field observations of free-living animals (IB, PA), and observations from Mr. Guido Parra (Tropical Environment Studies and Geography, James Cook University), from central and northern Queensland (Parra and Corkeron 2001, Parra *et al.* 2002).

### *Molecular Analyses*

Twenty-eight *Orcaella* tissue samples were collected between 1990 and 2001 from animals that were either stranded or taken incidentally in fishing operations. Four samples were obtained from northeast Australia and 24 samples were obtained from several locations throughout southeast Asia (Appendix 2). Tissue samples were stored in a 20% dimethyl sulfoxide (DMSO) solution saturated with NaCl (Amos and Hoelzel 1991) and included 27 skin tissue samples and one muscle tissue sample. All samples are archived in the Southwest Fisheries Science Center's Molecular Genetic Tissue Archive, La Jolla, CA.

Total genomic DNA was extracted using a lithium chloride (LiCl) extraction protocol modified from Gemmel and Akiyama (1996). Amplification and sequencing of the mitochondrial control region (D-loop) employed standard protocols (Palumbi *et al.* 1991, Saiki *et al.* 1988). The primers H16498 (5'-cctgaagtaagaaccagatg-3'; Rosel *et al.* 1994) and L15812 (5'-cctccctaagactcaagg-3'; developed at SWFSC) were used for both amplification and sequencing. Sequencing products were run on an Applied Biosystems Inc. Model 377 automated sequencer and were aligned by eye using SeqEd, version 1.0.3 software (ABI 1992).

Bootstrap analyses were performed using neighbor-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) analyses with Phylogenetic Analysis Using Parsimony software (PAUP 4.0, Swofford 1993). Unique haplotypes were used to create a bootstrap consensus tree using neighbor-joining analysis. A sequence of a killer whale (*Orcinus orca*) was used as the outgroup, as it is the closest relative to *Orcaella* (Gretarsdottir and Arnason 1992, LeDuc *et al.* 1999).

## RESULTS

### *External Morphometrics*

External measurements are displayed in Table 1. Mann-Whitney *U* tests revealed statistically significant differences ( $P = 0.001$ ) between regions in measurements of: tip of upper jaw to gape (UJGAP), tip of upper jaw to flipper (UJFLIP) and dorsal fin height (DFHEI). There were also significant differences ( $P = 0.05$ ) in total length (TLEN), tip of upper jaw to eye (UJEYE), length of anterior margin of flipper (AMFLIP) and maximum flipper width (MAXFL) measurements. Based on these univariate analyses, there were no other statistically significant differences in external measurements between regions (Table 1).

A PCA was run on 13 Australian and nine Asian specimens, comparing nine measurements. The first three axes accounted for a total of 67.2% of the variation (Fig. 1, Table 2). Based on the eigenvectors (Table 3), Asian specimens were pri-

Table 1. External morphometrics of Australian and Asian *Orcella*. All values (apart from total length, TLEN, in centimetres) are proportions of total length and used in the subsequent analyses. The mean proportion is followed by standard error (SE), sample size ( $n$ ), range and statistical significance (ns = not significant ( $P > 0.05$ ), \* = significant ( $P \leq 0.05$ ) and \*\* = highly significant ( $P \leq 0.001$ )). Acronyms for the measurements included in the analyses are as follows, with the numbers in brackets corresponding to measures in Norris (1961): TLEN = total length (1); UJEYE = tip of upper jaw to eye (2); UJGAP = tip of upper jaw to gape (4); UJEAR = tip of upper jaw to ear (5); EYEAR = eye to ear (6); UJBLOW = tip of upper jaw to blowhole (9); UJDOR = tip of upper jaw to dorsal fin (10); UJFLIP = tip of upper jaw to flipper (11); UJUMB = tip of upper jaw to umbilicus (12); UJGEN = tip of upper jaw to genital slit (13); UJANU = tip of upper jaw to anus (14); AMFLIP = anterior margin of flipper (29); FLIPTA = flipper tip to axilla (30); MAXFL = maximum flipper width (31); DFHEI = dorsal fin height (32); DFLEN = dorsal fin length (33); WTAIL = width of tail (34).

Measure	<i>Orcella beinsobni</i>			<i>Orcella brevirostris</i>			Mann-Whitney			
	Mean	SE	n	Range	Mean	SE	n	Range	U test results	Significance
TLEN	217.9	3.44	22	186.0–270.0	205.1	5.60	20	173.0–275.0	$P = 0.049$	*
UJEYE	6.8	0.23	18	5.2–9.1	8.2	0.34	12	5.5–10.2	$P = 0.003$	*
UJGAP	5.4	0.23	18	3.7–7.4	6.9	0.36	14	4.8–9.8	$P = 0.001$	**
UJEAR	10.3	0.59	13	4.9–12.3	12.3	0.78	7	8.9–14.8	$P = 0.052$	ns
EYEAR	4.2	0.40	11	3.1–7.3	3.9	0.21	6	3.3–4.6	$P = 0.615$	ns
UJBLOW	7.5	0.58	18	3.8–11.5	7.9	0.70	16	4.8–12.8	$P = 0.945$	ns
UJDOR	57.1	0.64	18	52.9–63.0	58.6	0.91	18	49.3–66.5	$P = 0.125$	ns
UJFLIP	18.7	0.38	20	14.4–23.0	20.5	0.40	15	17.0–23.9	$P = 0.001$	**
UJUMB	39.1	0.77	11	36.7–44.9	46.0	1.54	8	39.3–55.0	$P = 0.051$	ns
UJGEN	57.3	1.14	14	51.3–63.6	60.0	1.04	12	52.1–65.0	$P = 0.150$	ns
UJANU	64.5	0.81	16	54.0–67.7	66.8	1.35	12	57.9–74.5	$P = 0.085$	ns
AMFLIP	16.9	0.32	19	14.2–19.8	17.9	0.57	18	11.8–22.2	$P = 0.026$	*
FLIPTA	14.2	0.40	20	9.3–16.7	13.5	0.89	10	7.2–16.2	$P = 0.930$	ns
MAXFL	6.6	0.15	19	4.8–7.5	7.3	0.31	15	4.6–9.5	$P = 0.018$	*
DFHEI	4.4	0.14	16	3.4–5.3	3.0	0.12	18	2.1–4.0	$P = 0.000$	**
DFLEN	8.2	0.43	18	5.4–13.3	8.0	0.34	18	5.3–10.4	$P = 0.927$	ns
WTAIL	29.0	0.89	17	23.7–35.6	28.2	0.61	18	22.9–33.5	$P = 0.597$	ns

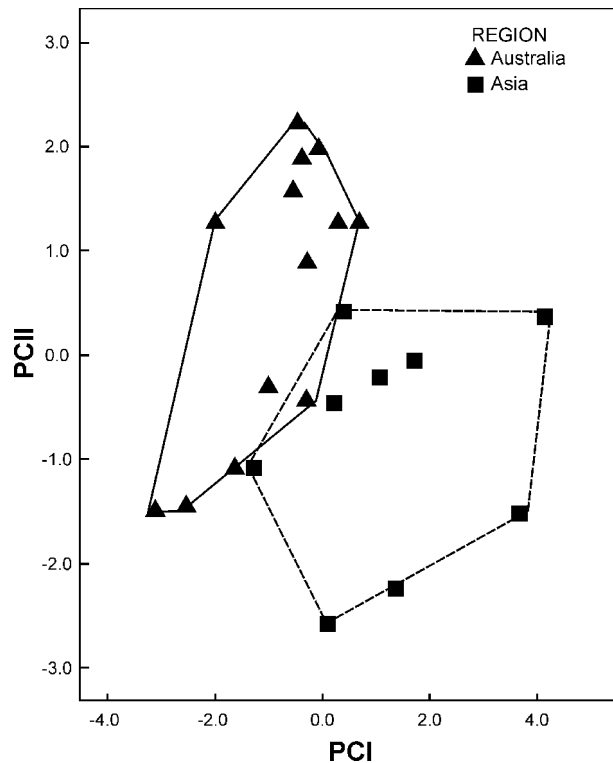


Figure 1. Results from a principal component analysis on external morphometrics of *Orcaella* using a subset of specimens with no missing values, from Australia ( $n = 13$ ) and Asia ( $n = 9$ ); see text for details.

marily characterized by smaller dorsal fin heights, larger maximum flipper widths, and larger distances between the tip of upper jaw to gape measurements (axis one). Australian specimens were characterized by smaller distances between the tip of upper jaw to flipper and larger tail width measurements (axis two) (Fig. 1).

Although the sample size of Asian specimens was small ( $n = 9$ ), a stepwise DFA ( $F = 3.84$  to enter and  $F = 2.71$  to remove) was conducted to examine potential differences in measurements between regions. A highly significant difference was found between the two regions (Wilks' Lambda 0.172,  $\chi^2 = 33.450$ ,  $P < 0.001$ ). Dorsal fin height was identified through the DFA as the best measure that distinguishes the Australian region from the Asian region—Australian specimens having a significantly larger dorsal fin than Asian specimens. The second variable selected by the stepwise DFA was maximum flipper width, where the Asian specimens had significantly larger flipper widths. Group prediction using cross-validation based on a discriminant analyses on these two variables classified 93.3% of the sample to the correct region, with two Asian samples being incorrectly classified during cross-validation.

Using descriptive statistics with the full data set, dorsal fin height was also identified as highly significantly different (Mann-Whitney  $U$  test,  $Z = -4.729$ ,  $P <$

Table 2. Eigenvalues and proportion of variance explained by each of the four axis, resulting from the principal component analysis on the reduced data set of specimens (13 Australian and nine Asian specimens).

Axis	Eigenvalue	% of variance	Cumulative % of variance	B-s Eigenvalue
1	2.894	32.153	32.153	2.829
2	1.915	21.278	53.431	1.829
3	1.235	13.720	67.172	1.329
4	1.062	11.804	78.955	0.996

0.001) and maximum flipper width identified as significantly different (Mann-Whitney  $U$  test,  $Z = -2.359$ ,  $P = 0.180$ ) (Table 1).

#### Total Length

Statistically significant differences were found in total length between regions (Mann-Whitney  $U$  test,  $Z = -1.967$ ,  $P = 0.049$ ), with Australian specimens being larger than Asian specimens. There was no evidence of sexual dimorphism in total length measurements of the unpooled (Australia: Mann-Whitney  $U$  test,  $Z = -0.405$ ,  $P = 0.685$ , Asia: Mann-Whitney  $U$  test,  $Z = -0.489$ ,  $P = 0.625$ ) datasets. Arnold and Heinsohn (1996) noted that the largest Australian specimens were all male; similarly, of the four largest Asian specimens, three were male (229.0–275.0 cm), with one 228.0 cm female from the Mekong River, Cambodia (Appendix 1; Asia 55). There is a suggestion of sexual dimorphism in both regions, with males growing larger than females, however further specimens need to be examined.

#### Other External Measurements

Resulting from the descriptive statistics, apart from dorsal fin height, the other highly significantly ( $P \leq 0.001$ ) different external measurements were tip of upper jaw to gape and tip of upper jaw to flipper. Of the nine measurements included in the

Table 3. The first three eigenvectors from the principal component analysis of Australian versus Asian specimens (Fig. 1) based on a reduced dataset of specimens (13 Australian and nine Asian specimens) with no missing values.

Measure	PCI	PCII	PCIII
UJGAP <sup>a</sup>	0.4886	-0.1662	0.1250
UJFLIP	0.4000	-0.2707	-0.0903
UJBLOW	0.0970	0.0306	0.5756
UJDOR	0.1942	-0.0600	-0.5057
AMFLIP	0.4575	-0.0280	0.3387
MAXFL	0.4909	0.2537	0.0408
DFHEI	-0.1536	0.5871	0.3575
DFLEN	0.2567	0.4330	-0.2781
WTAI	0.1202	0.5452	-0.2603

<sup>a</sup> See Table 1 for variable names.

stepwise DFA, only maximum flipper width was selected as indicating variation between regions (after dorsal fin height). This feature was also identified as being significantly different ( $P \leq 0.05$ ) in the descriptive statistics (along with tip of upper jaw to eye). However, due to the highly significant differences (as indicated by univariate analyses) in tip of upper jaw to flipper and tip of upper jaw to gape, it would have been expected that either of these two measurements would have been selected in the DFA, over flipper width. It may be that the small sample size in the multivariate analysis results in inadequate documentation of any secondary variation between regions.

### *Coloration*

Coloration patterns varied between the two forms. Observations of live individuals throughout Asia and fresh carcasses, confirmed a two-tone coloration pattern—uniform dark slaty gray (shades of gray varying considerably between individuals) on both dorsal and lateral fields (Fig. 2a, b), with a pale-colored ventral field extending forward to the lower chin and posteriorly to the anterior of the anus (Fig. 3a). The light ventral field extends as a sharply defined field onto the underside of the flippers. This extension is clearly visible in captive individuals (Fig. 3a), as well as freshly stranded individuals from Asia (Fig. 3b).

The tri-partite coloration of Australian *Orcaella*, with a distinct dorsal cape (Arnold and Heinsohn 1996) has been confirmed by subsequent observations on the central and northern Queensland coast (Parra and Corkeron 2001; Parra, unpublished data) and is shown in Figure 2c, d.

### *Molecular Analyses*

A 403-base sequence of the control region was obtained for all 28 samples. There were nine unique haplotypes identified: three from Australia and six from Asia. Thirty-four variable sites were found. There were 16 fixed base pair differences (one insertion/deletion, two transversions and 13 transitions) found between the Australian and Asian animals.

The bootstrap consensus tree using NJ is presented in Figure 4. The numbers on the nodes with three values represent bootstrap values for NJ, MP, and ML analyses, respectively. Other nodes are presented by NJ values only, because not all trees were drawn identically. The Australian animals separated from the Asian animals 100% of the time in all three analyses (NJ, MP, and ML) and were reciprocally monophyletic. The analysis also demonstrated strong support for two clades within the animals sampled from Asia, with the Laos/Cambodia animals from the upper Cambodian Mekong River (freshwater habitat) forming one clade and the animals from Thailand, Indonesia, and the Philippines (marine and freshwater habitats) forming the other clade.

The actual numbers of base pair differences between all haplotypes and the outgroup are listed in Table 4. The base pair differences between the Australian and Asian animals are highlighted in bold. The average number of base pair differences between the Australian and Asian samples was 24 base pairs or 5.9%. Within the animals sampled from Australia, the average number of base pair differences was five (1.2%) and within the animals sampled from Asia, the average number of base pair differences was six (1.5%).



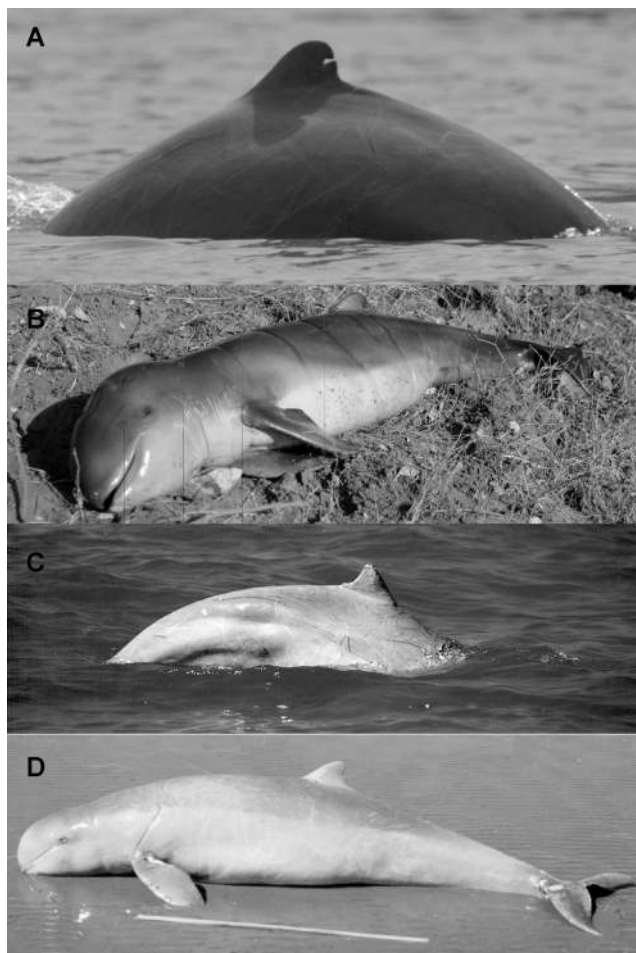


Figure 2. External coloration. *Orcaella brevirostris* (live animal, Mekong River, Cambodia: Fig. 2a); *O. brevirostris* (stranded animal, Mekong River, Cambodia: Fig. 2b); *O. heinsobni* (live animal, Cleveland Bay, Townsville, Australia (photo: Guido Parra): Fig. 2c) and *O. heinsobni* (animal that died after being accidentally caught in a shark net, Townsville, Australia [photo: George Heinsohn]: Fig. 2d).

#### TAXONOMIC TREATMENT

Class Cetacea Brisson, 1762  
 Family Delphinidae Gray, 1821  
 Genus *Orcaella* Gray, 1866  
*O. brevirostris* (Owen in Gray 1866)

#### *Synonymy*

From Stacey and Arnold (1999): *Phocaena (Orca) brevirostris* Owen in Gray (1866: 285). Type locality: “east coast of India, the harbour of Vizagapatam”

[Vishakhapatnam]. *Orcaella fluminalis*<sup>1</sup> Anderson in Gray, 1871: 80. Type locality “River Irawady.”

#### *Holotype*

BMNH 1865.4.20.1; skull from Vizagapatam, India.

#### *Specimens Examined*

External morphometrics: 34 specimens (see Appendix 1: Asian specimens, Appendix 3); Skull morphology: 77 specimens (see Appendix 3); DNA: 24 samples (see Appendix 2: all specimens except Laboratory Number 2905, 2906, 2907, 17365, Appendix 3). Specimens described and figured in the literature are included in Appendix 4.

#### *Description*

Owen (1866) and Owen (in Gray 1866) provided a very detailed description of the skull of the holotype; additional information was included in Anderson (1879). The holotype skull was figured by Arnold and Heinsohn (1996) and measurements of the holotype skull (as well as Anderson’s material of “*O. fluminalis*” were included in the analysis by Beasley *et al.* (2002a). Postcranial osteology was described and figured in the articles included under “Remarks.” Differences between *O. brevirostris* and *O. heinsobni* are discussed under the latter species.

Anderson (1879) also provided detailed information on the external morphology and internal anatomy. External morphometrics of *O. brevirostris* (including Anderson’s material of “*fluminalis*”) were provided in Arnold and Heinsohn (1996: table 7), and summary statistics, including 11 new specimens, are provided in Table 1. Differences between *O. brevirostris* and *O. heinsobni* are discussed under the latter species.

Coloration of *O. brevirostris* is two-tone, with a dark slaty gray dorsal and lateral field, and a pale ventral field (Anderson 1871, 1879; Bonhote 1903; Mörzner Bruyns 1966; this paper). Animals in captivity from the Mahakam River, east Kalimantan (observed at Jaya Ancol Oceanarium, Djakarta, Indonesia) were described as being lightly colored and subtly two-tone (Stacey and Arnold 1999) and very light, almost white in color (Beasley and Jefferson 1997). However, this overall light coloration is likely due to the animals described being kept solely indoors for many years at Jaya Ancol Oceanarium (Tas’an and Leatherwood 1984), thereby reducing their pigmentation and resulting in a whitish coloration. A dorsal groove extends from behind the neck crease to just before the dorsal fin (Fig. 5). This feature was

<sup>1</sup> Although the authority for *O. fluminalis* has been cited as Anderson, 1871 (an article in the *Proceedings of the Zoological Society of London*), Hershkovitz (1966) cited Gray 1871 (*Supplement to the Catalogue of Seals and Whales in the British Museum*). A bibliography of Gray’s publications (Gray 1875) lists the *Supplement* as the first entry for 1871, suggesting it appeared early in that year (J. Mead, personal communication). Gray (1871, p. 80) attributed the name *fluminalis* to “Anderson’s MS & Icon. Ined.”; Anderson’s article was received on 7 February 1871 and would have appeared later that year. Thus circumstantial evidence suggests Hershkovitz was correct in giving priority to Gray’s 1871 publication and we accept that decision. However, since the name and diagnosis were clearly attributed by Gray to Anderson’s account, the authority would be Anderson in Gray, 1871 (see also discussions on nomenclature in Arnold and Heinsohn (1996): 204; Stacey and Arnold (1999): 1, 6).

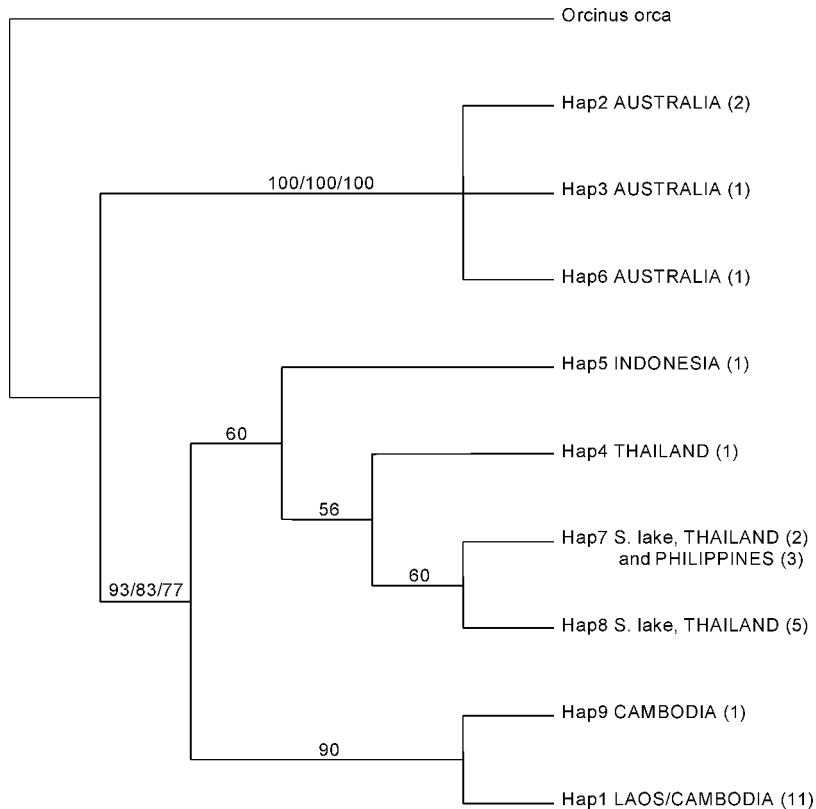


Figure 3. A captive *Orcaella brevirostris* from the Gulf of Thailand, showing the characteristic extension of the pale ventral field onto the flipper and light ventral field (Fig. 3a) and a freshly stranded newborn *O. brevirostris* from the Mekong River, Cambodia, showing the characteristic extension of the pale ventral field onto the flipper (Fig. 3b).

initially observed in the Mahakam River population (Stacey and Leatherwood 1997). It has been observed by the first author in live individuals from coastal Cambodia, Chilika Lagoon (India), Malampaya Sound (Philippines), east and west Malaysia, Songkhla Lake (Thailand) and in the Mekong River freshwater population (Cambodia and southern Laos).

#### *Distribution*

Northwest Bay of Bengal, possibly south to Madras (Chennai) (Miller 1997, Sathasivam 2002), through to southern Indonesia (Java) and northeast to southwest Philippines (Malampaya Sound, Palawan Island). Freshwater populations are found



*Figure 4.* Bootstrap consensus tree resulting from neighbor joining (NJ) analysis. The numbers on the nodes represent bootstrap values for NJ/Maximum parsimony/Maximum likelihood analyses, respectively. Only the NJ value is given for those nodes where the MP and ML trees differed from the NJ tree. All three analyses supported a reciprocally monophyletic relationship between the Australian and Asian animals. The numbers in parentheses represent the number of animals found to have that particular haplotype.

in the Ayeyarwady River—up to 1,500 km upstream (Myanmar [Burma]), Mekong River—up to 690 km upstream (Vietnam, Cambodia, southern Laos), and the Mahakam River–Semayang Lake system—up to 560 km upstream (east Kalimantan, Indonesia). Detailed distribution can be found in Stacey and Leatherwood (1997) with additional Philippines records in Dolar *et al.* (2002).

#### *Variation*

Anderson (1871, 1879) recognized two species in the genus; *O. brevirostris* in marine waters (“confined as far as at present known to the Bay of Bengal, and to frequent the estuaries of the larger rivers falling into it,” Anderson 1879: 369) and *O. fluminalis* in the Irrawaddy [Ayeyarwady] River. However, the reality of the alleged differences between them was questioned or denied by a number of authors (Thomas 1892, Weber 1923, Pilleri and Gahr 1973–1974, Lloze in Marsh *et al.* 1989),

Table 4. Number of base pair differences between *Orcaella* haplotypes and the outgroup. The base pair differences between the Australian and Asian animals are highlighted in bold for reference.

	Base pair differences									
	1	2	3	4	5	6	7	8	9	10
1 <i>Orcinus orca</i>	—									
2 Hap2 Australia	42	—								
3 Hap3 Australia	43	4	—							
4 Hap6 Australia	41	3	7	—						
5 Hap5 Indonesia	36	25	26	28	—					
6 Hap4 Thailand	34	23	24	24	8	—				
7 Hap7 SLThai/Philippines	36	23	26	24	8	2	—			
8 Hap8 SLThailand	37	24	27	25	7	3	1	—		
9 Hap9 Cambodia	35	20	23	21	12	8	6	7	—	
10 Hap1 Laos/Cambodia	36	21	24	22	11	7	5	6	1	—

and Ellerman and Morrison-Scott 1951 reduced them to subspecific rank as *O. b. brevirostris* Gray, 1866 and *O. b. fluminalis* Anderson, 1871.

Our genetic data demonstrated support for two clades within Asia, *i.e.*, the Mekong River samples from Cambodia and southern Laos, and all others (from marine and freshwater sites in Thailand, Indonesia and Philippines) (Fig. 4). However, there was no clear support for separation of specimens from freshwater sites versus those in marine habitats. Within the Thailand/Indonesia/Philippine clade, the animals from Songkhla Lake in Thailand group together and share a haplotype with the Philippines animals. However, they appeared to be more closely related to the animal located from coastal waters of Trat Province, Thailand (eastern Gulf of Thailand), than the freshwater animal from the Mahakam River in Indonesia. The low bootstrap support (60%) for the Asian clade containing both marine and freshwater animals may indeed be an indication that additional samples need to be examined to help clarify if distinct populations of *Orcaella* exist in different habitats, or if there is separation by geographic area only.

The Mahakam River (east Kalimantan) population has not been formally named, however several characters of potential taxonomic significance have been described. A dorsal groove was described in Stacey and Leatherwood (1997), however this appears to be a more general feature of *O. brevirostris* (see our description above). Tas'an *et al.* (1980)<sup>2</sup> reported that in the Mahakam River population the teeth remain buried in the gum, even in adult animals.

Smith and Hobbs (2002: appendix 1) summarized the characters for "*O. fluminalis*," proposed by Anderson (1871, 1879) for dolphins from the Ayeyarwady River. It has been previously suggested that any discussion of the validity of that taxon must be based on animals from the type locality; this suggestion is reinforced by the hints of divergence within freshwater habitats based on our molecular data. As with previous reviewers (Lloze 1973, Pilleri and Gehr 1973–1974), we have no further morphological or genetic data from the Ayeyarwady River and thus cannot address the

<sup>2</sup> Tas'an, A. Irwandy, Sumitro and S. Hendrokusumo. 1980. *Orcaella brevirostris* (Gray, 1866) from the Mahakam River. Unpublished report. Jaya Ancol Oceanarium, Jakarta.



Figure 5. Specimen of *Orcaella brevirostris* showing the characteristic dorsal groove from a free-living individual (Mekong River, Cambodia: Fig. 5a) and a stranded individual (Mekong River, Cambodia: Fig. 5b). *O. heinsobni* showing neck crease and lack of dorsal groove (Cleveland Bay, Townsville, Australia: Fig. 5c).

validity of *O. fluminalis*. Additional work is necessary to clarify the taxonomic status of *Orcaella* in the Ayeyarwady River and other Asian freshwater habitats.

#### *ORCAELLA HEINSOHNI* NEW SPECIES

##### *Holotype*

QM JM4721 (JCU MM61). Skull, mandibles, right and left tympano-periotic bones, right scapula, incomplete left flipper bones (some phalanges missing), loose teeth. From a 214.0 cm male, with 11.5 dentinal growth layers, collected from a

shark net in Horseshoe Bay, Magnetic Island, Queensland, Australia, on 21 April, 1972 by G. Heinsohn and A. Spain.

The holotype skull was illustrated in Arnold and Heinsohn (1996, fig. 5, 9, 11). No genetic sequence data are currently available from the holotype.

#### *Paratypes*

QM JM 4726 (JCU MM 82). Skull, mandibles, right and left tympano-periotic bones, right scapula, hyoid, left humerus, radius, ulna, incomplete carpals and phalanges. From a 222.0-cm female with 17 dentinal growth layers, collected on a beach near Three Mile Creek, Townsville, Queensland, Australia, on 18 August 1974, by G. Heinsohn and T. Heinsohn.

USNM 284430. Skull from dolphin of unknown sex, "picked up at native camp site" at Melville Bay, Cape Arnhem Peninsula, Northern Territory, Australia, on 16 July, 1948. Illustrated in Johnson (1964, plate 14, 15).

#### *Specimens Examined*

External morphometrics: 25 specimens (see Appendix 1: Australian specimens, Appendix 5); Skull morphology: 46 specimens (see Appendix 5); DNA: 4 specimens (see Appendix 2: Laboratory Numbers 2905, 2906, 2907, 17365, Appendix 5). Specimens described and figured in the literature are included in Appendix 6.

#### *Diagnosis*

*Morphological*—Head rounded in lateral view, usually bounded by distinct neck crease (commonly indistinct in *O. brevirostris*), dorsal groove lacking (dorsal groove present in front of dorsal fin in *O. brevirostris*, see above and Fig. 5), proportional dorsal fin height statistically significantly greater than in *O. brevirostris* with mean = 4.4% (range 3.4%–5.3%,  $n = 16$ ) *cf.* mean = 3.0% (range 2.1%–4.0%,  $n = 18$ ) in *O. brevirostris*; coloration subtly three-tone, with distinct dorsal cape (cape absent in *O. brevirostris*); vertex with mean = 3 (range 0–6) bony ossicles (two nasal bones in *O. brevirostris*, only a single specimen with an additional ossicle) (Fig. 6); mesethmoid plate reduced and generally in advance of the anteriormost nasal ossicle, leaving large area of frontal bone exposed (central portion mesethmoid plate usually extending behind the anteriormost point of nasal bones, with only small area of frontal bone between nasal bones exposed in *O. brevirostris*) (Fig. 6); supernumerary bone may be present between nasal ossicles and posterior border of mesethmoid (supernumerary bone absent in *O. brevirostris*); length of antorbital process greater than in *O. brevirostris* with mean = 38.6 mm (range 31.8–53.2,  $n = 40$ ) *cf.* mean = 26.3 mm (range 17.0–32.6,  $n = 50$ ) in *O. brevirostris*; temporal fossa height greater than in *O. brevirostris* with mean = 61.2 mm (range 49.1–83.2,  $n = 41$ ) *cf.* mean = 45.8 mm (range 33.0–55.3,  $n = 53$ ) in *O. brevirostris* (Fig. 7); pterygoid hamuli with medial flanges, more closely opposed than in *O. brevirostris* with mean = 4.0 mm (range 1.6–9.8,  $n = 32$ ) *cf.* mean = 14.5 mm (range 7.9–20.7,  $n = 38$ ) in *O. brevirostris* (Fig. 8); pterygoid depth smaller than in *O. brevirostris* with mean = 24.5 mm (range 19.4–31.2,  $n = 31$ ) *cf.* mean = 38.1 mm (range 30.7–48.6,  $n = 33$ ) in *O. brevirostris* (Fig. 8). See Appendix 7 for further details.



Figure 6. Vertex region of *Orcaella heinsobni* in a specimen from Australia (QMJM4740, MM1013) (Fig. 6a) and *O. brevirostris* from Malaysia, Asia (BMNH 1964.2.24.1) (Fig. 6b). Note the larger number and smaller width of nasal ossicles, the reduced mesethmoid plate and exposed frontal bone (with supernumerary bone) on the vertex of *O. heinsobni*.

*Molecular*—Based on a 403 base segment of the mtDNA control region, there are 17 diagnostic sites with 16 fixed base pair differences and one insertion/deletion that distinguish *O. heinsobni* from *O. brevirostris* (Table 5).

#### *Description*

Males to 270.0 cm; females to 230.0 cm, based on 37 animals. The mass of three adults (2.14–2.25 m long) was recorded as 114–133 kg (Arnold and Heinsohn 1996). Head broadly rounded in lateral view and lacking beak. Nape usually with a distinct neck crease about half way between the eye and anterior insertion of the flipper. Snout to dorsal fin lacks dorsal groove (Fig. 5). Dorsal fin situated in latter





Figure 7. Differences in temporal fossa height between a specimen of *Orcaella heinsobni* from Australia (NMNH 284429) (above) and *O. brevirostris* from the Mahakam River, Indonesia, Asia (NMNH 1999743) (below).

half of body (upper jaw to dorsal fin tip mean = 57.1% (range 52.9–63.0%,  $n = 18$ ) of body length). Anterior flipper length mean = 16.9% (range 14.2–19.8%,  $n = 19$ ), maximum width (middle of flipper): mean = 6.6% (range 4.8%–7.5%,  $n = 19$ ) of body length. Dorsal fin height mean = 4.4% (range 3.4%–5.3%,  $n = 16$ ) of body length, dorsal fin length mean = 8.2% (range 5.4%–13.3%,  $n = 18$ ) of body length. Tail fluke width mean = 29% (range 23.7%–35.6%,  $n = 17$ ). See Table 1 for additional descriptive statistics.

Color subtly three-tone, with dark cape (Fig. 2c, d; Arnold and Heinsohn 1996: fig. 2, 3), white abdominal field (Arnold and Heinsohn 1996: fig. 2–4) and intermediate light gray to brownish gray field on the side (Arnold and Heinsohn 1996: fig. 2, 3; Parra and Corkeron 2001: fig. 2).

Condylbasal length mean = 306.4 mm (range 287.2–334.8,  $n = 41$ ); greatest postorbital width mean = 203.2 mm (range 187.1–214.5,  $n = 42$ ); rostral length mean = 135.4 mm (range 120.9–149.0)/mean = 44.2% of condylbasal length (range 42.1%–46.2%,  $n = 40$ ); mean number of teeth/alveoli (range in parentheses) UR:18.3 (16–20), UL:18.0 (11–22), LR:16.8 (14–18), LL:17.3 (15–19); all mean values significantly larger than in *O. brevirostris* (Beasley *et al.* 2002a: appendix 2, Arnold and Heinsohn 1996: fig. 13, Stacey and Arnold 1999: fig. 2). Supernumerary bone may be present within exposed frontal bone, anterior to medial nasal ossicles (Johnson 1964: plate 14; Arnold and Heinsohn 1996: fig. 5, 6). Length of antorbital process mean = 38.6 mm (range 31.8–53.2,  $n = 40$ ), height of temporal fossa mean = 61.2 mm (range 49.1–83.2,  $n = 41$ ) (Beasley *et al.* 2002a: fig. 7); nasal

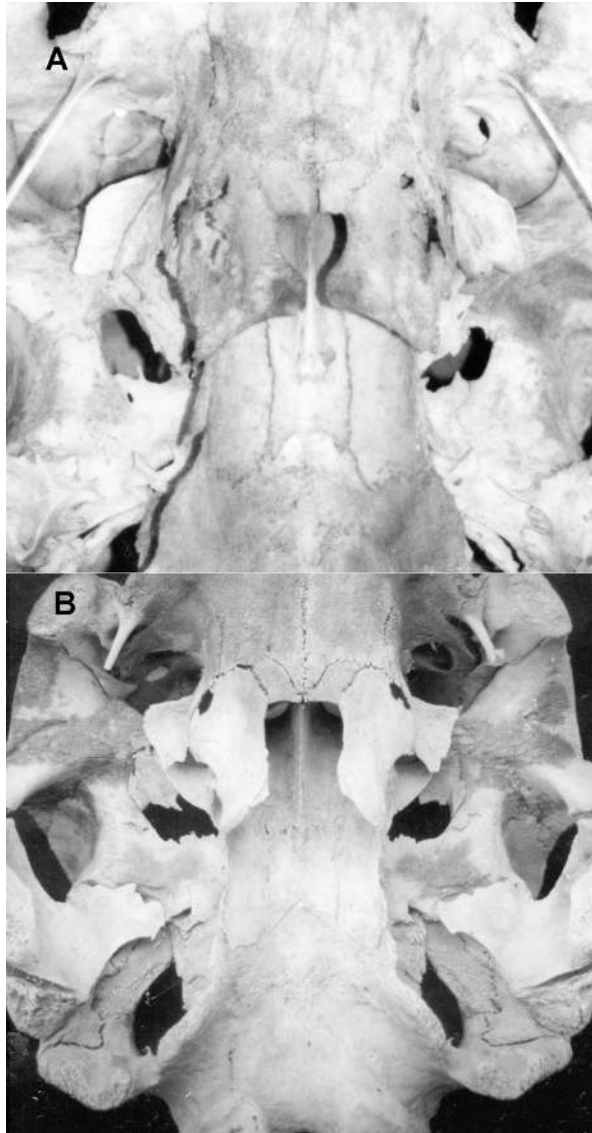


Figure 8. Pterygoid region of *Orcaella beinsobni* from Australia (QMJM4721) (Fig. 8a) and *O. brevirostris* from the Mekong River, Cambodia (Fig. 8b). Note the medial flanges on the pterygoid hamuli of the Australian specimen *O. beinsobni*, with narrower separation of the hamuli.

ossicles, mean = 3 (range 0–6,  $n = 37$ ) (Arnold and Heinsohn 1996: fig. 6–8, Beasley *et al.* 2002a: fig. 10A); separation between posterior margin of mesethmoid plate and antermost point of nasal bone/ossicle mean = 4.6 mm (range –3.8–12.3,  $n = 33$ ) (Arnold and Heinsohn 1996: fig. 6–8 and 15, Beasley *et al.* 2002a: fig. 10A); minimum separation of pterygoid hamuli mean = 4.0 mm (range 1.6–9.8,  $n = 32$ )

Table 5. The 17 diagnostic sites separating *Orcaella heinsobni* and *O. brevirostris*. The base number represents the base position in the 403 base sequence. The start position of the 403 base region that was sequenced corresponds to position 15891 of the fin whale, *Balaenoptera physalus*, sequence published by Arnason *et al.* 1991.

Base number	Diagnostic sites																
	1	1	2	2	2	2	2	3	3	3	3	3	3	3	3	3	
	3	5	6	7	8	9	9	0	1	4	4	4	4	5	6	6	8
	5	8	5	6	3	6	7	9	7	0	2	3	7	1	1	5	6
Hap2 Australia	T	A	T	G	A	C	A	G	T	C	G	G	T	C	G	C	A
Hap3 Australia	T	A	T	G	G	C	A	G	T	C	G	G	T	C	G	C	A
Hap6 Australia	T	A	T	G	A	C	A	G	T	C	G	G	T	C	G	C	A
Hap5 Indonesia	G	G	A	A	—	T	G	A	A	T	A	A	C	T	A	T	G
Hap4 Thailand	G	G	A	A	—	T	G	A	A	T	A	A	C	T	A	T	G
Hap7 SLThaiPhil	G	G	A	A	—	T	G	A	A	T	A	A	C	T	A	T	G
Hap8 SLThailand	G	G	A	A	—	T	G	A	A	T	A	A	C	T	A	T	G
Hap9 Cambodia	G	G	A	A	—	T	G	A	G	T	A	A	C	T	A	T	G
Hap1 LaosCamb	G	G	A	A	—	T	G	A	G	T	A	A	C	T	A	T	G

(Arnold and Heinsohn 1996: fig. 10–12, Stacey and Arnold 1999: fig. 2, Beasley *et al.* 2002a: fig. 12A); depth of pterygoid mean = 24.5 mm (range 19.4–31.2,  $n = 31$ ) (Beasley *et al.* 2002a: fig. 12). Descriptive statistics of other cranial measurements are provided in Beasley *et al.* (2002a): appendix 2.

Vertebral formula C7, T12–13, L9–12, Ca28–30+ = 58–61, ( $n = 6$ ) with 17–20 chevrons (Arnold and Heinsohn 1996: fig. 49–54). Ribs 12–13, with 7–8 of those bicipital. Scapula with acromion process usually larger than coracoid process (Arnold and Heinsohn 1996: fig. 57), though may be subequal. Sternum with broadly concave anterior margin; sternum remains compound even in mature animals (Arnold and Heinsohn 1996: fig. 55 A, B).

Tympanoperiotic bones attached to mastoid pad of zygomatic arch (Arnold and Heinsohn 1996: fig. 29–30). Tympanic bulla with hemispherical outer posterior prominence and deep interprominential notch; posterior process directed posteriorly to posterolaterally. Tractus spiralis foraminosis of periotic bone prominent; aequeductus vestibuli set at base of an extensive funnel-shaped depression bounded by spongy bone (Arnold and Heinsohn 1996: fig. 17–28, Stacey and Arnold 1999: fig. 3).

#### Etymology

Named for Dr. George E. Heinsohn, for his pioneering work on northeast Australian odontocetes, including the collection and initial analysis of *Orcaella heinsobni* specimens which form the basis for much of our knowledge of the new species.

#### Distribution

Confirmed records from Broome, Western Australia, the Northern Territory, and along the Queensland coast as far south as the Brisbane River (Stacey and Arnold 1999, Beasley *et al.* 2002a, Parra *et al.* 2002: appendix 1). One additional record from Daru, Papua New Guinea (Beasley *et al.* 2002a). Sight records

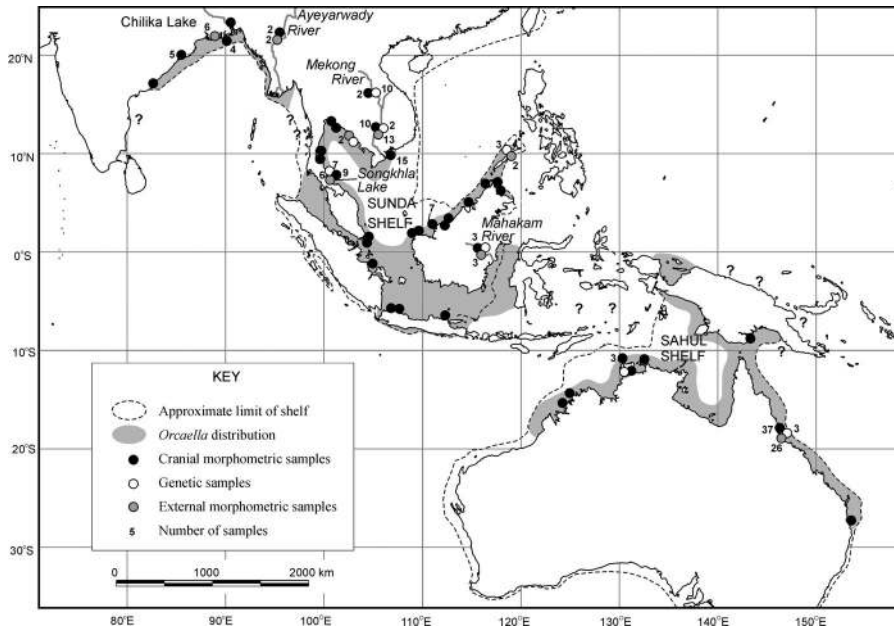


Figure 9. Map of Australia and Asia showing the range of *Orcaella* (shaded) based on literature records and the distribution of collection localities for specimens examined in Beasley *et al.* (2002b) and this study. The question marks denote areas where there is a lack of published records, resulting in questionable distribution. The extent of the Sahul and Sunda shelves are indicated by the dashed line.

indicate that these dolphins occur mainly in protected, shallow, coastal waters, especially adjacent to river and creek mouths (Parra *et al.* 2002). The expected range of *O. beinsobni* is the coastal zones of Australia and Papua New Guinea, as indicated by the shaded area in Figure 9, and Beasley *et al.* (2002a, fig. 1). Thus *O. beinsobni* occurs on the Sahul Shelf, whereas the distribution of *O. brevirostris*, as we restrict it, corresponds to the Sunda Shelf. These areas are separated by deep oceanic waters and remained separate even during periods of lowered sea levels in the Pleistocene Ice Ages (Woodland 1983, Holloway and Hall 1998, Randall 1998). The apparent gap in distributions of the two species (Stacey and Arnold 1999, Arnold 2002, Beasley *et al.* 2002a), based on published records, needs to be substantiated by further studies of distribution, particularly within the Indonesian archipelago.

#### Variation

The characteristics in skull morphology in *O. beinsobni* are consistent in specimens from throughout the range of the species (northwestern Australia to southern Queensland, plus southern Papua New Guinea,  $n = 46$ ) as indicated in Beasley *et al.* (2002a). The external morphometrics and color pattern are based on specimens from central and northern Queensland, while the molecular analysis includes specimens from Queensland and the Northern Territory, though with limited sample size ( $n = 4$ ).

### Remarks

There were statistically significant differences between Asian and Australian specimens in the number of teeth/alveoli in both upper tooth rows, as well as in the mandibles. This may relate to the significantly larger size of *O. heinsobni* skulls, as indicated by condylobasal length (Beasley *et al.* 2002a: appendix 2). Geographical and interspecific variation of tympanoperiotic bones remains undocumented.

The number of vertebrae in *O. heinsobni* (58–61,  $n = 6$ ) is smaller than reported for *O. brevirostris* (62–63,  $n = 4$ ; Anderson 1879, Lloze 1973). The acromion process of the scapula is usually larger than the coracoid process, while the opposite appears to be the usual case in *O. brevirostris* (Anderson 1879: plate 20; Lloze 1973: plate 30; Pilleri and Gahr 1973–1974: plate 26). The sternum of *O. heinsobni* remains compound even in mature animals; this has not been reported for *O. brevirostris* (Anderson 1879, Lloze 1973, Pilleri and Gahr 1973–1974). These may represent additional differences between the species, but are based on limited observations and need to be confirmed.

With the recognition of *O. heinsobni*, published information on *O. brevirostris* needs to be reviewed. The phylogenetic study by Gretarsdottir and Arnason (1992) was entirely based on *O. heinsobni*, while that of Arnold and Heinsohn (1996) and LeDuc *et al.* (1999) contained samples of both *O. brevirostris* and *O. heinsobni*. The data on osteology (table 1, Townsville data), feeding (Townsville data: p. 110 and table 2), as well as life history and reproduction (pp. 113–114) in Marsh *et al.* (1989) referred to *O. heinsobni*, as did data on abundance (Freeland and Bayliss 1989). Vocalizations documented by Van Parijs *et al.* (2000) refer to *O. heinsobni*; differences from vocalizations documented by Kamminga *et al.* (1983) in *O. brevirostris* from east Kalimantan, may reflect differences between the species, as well as geographical and habitat variation.

### Suggested Common Name

The general use of “Irrawaddy dolphin” for dolphins found in freshwater and marine habitats from the Bay of Bengal to eastern Australia has led to confusion in the past and is particularly inappropriate for Australian populations which are here considered a distinct species. Watson (1981) suggested “snubfin dolphin” as an alternate name. This name highlights a diagnostic external character, is appropriate to all populations, and has been included in lists of common names such as Rice (1998) and general field guides such as Carwardine and Camm (1995). For *O. heinsobni*, we suggest the name “Australian snubfin dolphin.” With only one cranial specimen from Papua New Guinea (showing consistent *O. heinsobni* features) (Beasley *et al.* 2002a), we cannot yet consider *O. heinsobni* an Australian endemic species; however, the common name reflects the fact that the majority of known specimens and all biological work are based on Australian populations. We hope that these findings will raise national awareness of this obscure dolphin, which was recorded from Australia only in the 1960s by an American mammalogist (Johnson 1964) and a Dutch sea captain (Mörzer Bruyns 1966).

### DISCUSSION

Discontinuities in particular characters (whether morphological, behavioral, or molecular) are the basis for diagnosing taxonomic entities, given at least an as-

sumption that the characters used are heritable and thus have a genetic basis. As noted by Helbig *et al.* (2002), the taxonomic inferences based on such discontinuities will vary according to the species concept adopted by taxonomists. For proponents of the biological species concept, the discontinuities represent a proxy for breeding trials in establishing reproductive isolation; discontinuities may equally provide evidence of prolonged lineage sorting over time which is fundamental to phylogenetic species concepts. Whether such discontinuities are accepted as evidence of a species or subspecies difference also depends at least partly on the species concept. Proponents of the biological species concept require that a higher proportion of specimens can be diagnosed consistently, compared with a subspecies, in which a greater degree of overlap in characters is accepted (see Mayr 1969 for examples). In phylogenetic studies, however, any taxon which can be diagnosed is considered as a species.

Such taxonomic inferences are relatively straightforward in sympatric or even parapatric populations. However, there are particular problems with allopatric populations, in which it is difficult to see how conclusive evidence for reproductive isolation or lineage integrity can be offered. The degree of divergence is the basis for a judgment on whether or not allopatric species would remain isolated should they become sympatric. Examples given by Milinkovitch *et al.* (2001) show that it is just as difficult making taxonomic inferences about allopatric populations based on discontinuities in molecular data, as it is using morphological data. As such, the assignment of species rank in allopatric populations is based on a hypothesis (Helbig *et al.* 2002), which may be difficult, if not impossible, to test. The implication from such studies is that the level of evidence for species recognition, based on geographical discontinuities in the data, must be greater when discussing allopatric populations. Helbig *et al.* (2002) suggested that allopatric populations (of birds) be assigned species rank if they "are fully diagnosable in each of *several* discrete or continuously varying characters related to different functional contexts, *e.g.*, structural features [often related to foraging strategy], colors [related to sexual selection and camouflage], vocalizations [related to communication], or DNA sequences, and the sum of the character differences corresponds to or exceeds the level of divergence seen in related species that coexist in sympatry."

Between *Orcaella* specimens from Australia and Asia, there are a number of differences in the external morphology, skull, color pattern, and genetic distance, with suggestions of additional characters in the postcranial osteology. However, intraspecific geographic variation in odontocetes has been demonstrated at a variety of scales (*e.g.*, Perrin 1975; Kitchener *et al.* 1990; Perrin *et al.* 1991, 1999; Dizon *et al.* 1994; Baker *et al.* 2002; Turner and Worthly 2003). Perrin (2002) noted that geographic variation within odontocetes can be considered to be universal. Historically, widely disjunct populations have been considered species, *e.g.*, the antitropical (Davies 1963) species pairs such as *Hyperoodon ampullatus/planifrons*, *Berardius bairdii/arnuxii*, *Lissodelphis borealis/peronii*, *Lagenorhynchus obliquidens/obscurus*, as well as the species of right whales *Eubalaena glacialis/japonica/australis*. Variation within widely and more continuously distributed taxa, such as the false killer whale *Pseudorca crassidens* and killer whale *Orcinus orca* (although refer to Pitman and Ensor (2003)), has tended to be considered intraspecific, while the status of geographical variants in the finless porpoise *Neophocaena phocaenoides* (Jefferson 2002), Indian and Pacific humpback dolphins (*Sousa chinensis/plumbea*) (Jefferson and Van Waerebeek 2004), or river dolphin *Platanista* (Rice 1998) remain unresolved.

Considered on their own, most of the differences in external characters that we

have demonstrated are within the range exhibited by subspecies of other dolphins. The differences in the dorsal fin and presence or absence of the dorsal groove in *Orcaella* are no greater than fin shape differences and presence or absence of a postanal hump in subspecies of *Stenella longirostris* (Perrin 1990), while color differences are much more marked in what are considered subspecies of *Phocoenoides dalli* (Amano and Miyazaki 1996).

The skull characters are more striking, although some of the most distinctive appear to be co-correlated and associated with the neoteny which is strongly developed in *Orcaella*, as evident in the extensive interparietal, which remains exposed on the vertex of the skull in adult specimens (Arnold and Heinsohn 1996). The poor development of the mesethmoid plate, presence of uncoalesced nasal ossicles (as well as, perhaps, the retention of the compound sternum) in Australian dolphins may be related to such neoteny. The uncoalesced nasal ossicles are known to occasionally occur in other cetacean species (*Stenella coeruleoalba*: Busnel *et al.* 1968) and at least one specimen of *O. brevirostris* (OBRE03: see Beasley *et al.* 2002a), from Sarawak, Malaysia, and one specimen from Chilika Lake, India (IB, unpublished data). However, uncoalesced nasal ossicles occur consistently in the Australian dolphins and can be considered a fixed character. The greater apparent expression of neotenic features in Australian dolphins could be considered a character in its own right. Other features, such as the difference in the separation of the pterygoids, are not obviously related to neoteny. In the combination of characters within a principal component analysis (Beasley *et al.* 2002a) the skulls of Australian specimens were unambiguously separated from all Asian specimens, including the holotype of *O. brevirostris* and specimens of "*fluminalis*" described by Anderson (1879).

The molecular analyses demonstrated clear genetic differentiation between *Orcaella* from northern Australia and Asia, thus supporting the results found above. The percent of base pair differences (5.9%) between the Australian and Asian populations is similar to that found by previous genetic work by LeDuc *et al.* (1999) (5.3%), using a small sample size and the cytochrome-B gene. This percent difference between populations is high and, according to Le Duc *et al.* (1999), was found to be greater than the interspecific and intergeneric comparisons within the subfamily Delphininae using cytochrome-B. Although the sample size of Australian specimens is small ( $n=4$ ), the genetic difference is great enough that the results probably would not change significantly with additional Australian specimens.

In order to examine this potential difference in mtDNA control region, 57 sequences of *Stenella coeruleoalba* and 89 sequences of *Delphinus delphis* (unpublished data, SWFSC) were compared. In a 406-base region, the average base pair difference between the two recognized species was 11 bases (range 3–18 bases), or 2.8%. This is less than half the difference found between the two *Orcaella* populations (average = 24, range 20–28). The average base pair difference between clades demonstrated in this paper was greater than within clade variation (1.2% for Australia, 1.5% for Asia). Although the sample sizes were small for both clades, animals from a wide geographic range within Asia and from both freshwater and marine habitats were represented.

Our analysis of DNA demonstrated clear genetic distance and reciprocal monophyly between the Asian and Australian samples. However, neither on their own are necessarily correlated with genetic isolation (Milinkovitch *et al.* 2001). In other species of dolphins, it is usually a concordance of characters that is used as evidence of species separation. Thus the pairs *Delphinus capensis/delphis* (Heyning and Perrin 1994, Rosel *et al.* 1994) or *Tursiops truncatus/aduncus* (Wang *et al.* 1999, 2000) were long recognized as showing differences in rostral length but it was only with other

characters (*e.g.*, color pattern and genetic distance) that these were considered of specific significance. The sympatric species *Globicephala melas/macrorhynchus* can be diagnosed by differences in flipper length, number of teeth and width of premaxillae on the rostrum (Ross 1984).

For *Orcaella*, we have demonstrated consistent and concordant, taxonomically significant differences between Asian and Australian dolphins in the presence or absence of dorsal groove, coloration patterns, development of mesethmoid plate and exposure of the frontal at the front of the cranium, presence or absence of supernumerary bones on the vertex, proportions of the pterygoid region, and marked genetic separation based on mitochondrial control region (consistent with previously reported results based on cytochrome-B: LeDuc *et al.* (1999)). Highly statistically significant differences (slightly overlapping sample ranges) existed in: dorsal fin height, number of nasal bones/ossicles, average width of nasal bones/ossicles, height of temporal fossa, length of antorbital process, depth of pterygoid notch and separation of pterygoid hamuli. Taxonomically significant differences also existed in vertebral count, as well as form of the scapula and sternum; however, these need to be confirmed in a larger number of specimens. It is this high concordance of characters that leads to a sum of character differences corresponding to, or exceeding, the level found in other odontocete species that coexist in sympatry and hence argues for a level of reproductive isolation and lineage sorting consistent with species separation.

### Conclusion

Clear and consistent differences between Asian and Australian specimens in coloration, cranial and external morphometrics, postcranial morphology and molecular data are consistent with species-level differences between these two regions. Cranial morphological features from one specimen from Papua New Guinea were consistent with those of *O. heinsobni*. However, further study is needed on *Orcaella* in Papua New Guinea and neighbouring regions. In addition, further morphological and genetic study is warranted, to determine if subspecies-level differences exist within Asian populations.

The species-level separation of *Orcaella brevirostris/heinsobni* has immediate conservation implications. As mentioned in Beasley *et al.* (2002a), the results presented in this study confirm that a single region, *e.g.*, northern Australia, cannot conserve the genetic diversity of *Orcaella*. Increased research and conservation efforts should be focused on both regions, where very little is currently known on basic biological and ecological aspects of either species. Based on recent research, various *Orcaella brevirostris* populations are in rapid decline, with all known riverine populations facing potential extirpation in the near future (see Introduction). As demonstrated by the molecular data, the potential for subspecies level differences among the riverine subpopulations make conservation efforts particularly significant and urgent.

### ACKNOWLEDGMENTS

We wish to thank again the many colleagues acknowledged in Beasley *et al.* (2002a) for providing access to skeletal material in their care. We particularly acknowledge George Heinsohn for his dedication in collecting Australian specimens, on which much of the knowledge of the new species is based, and for his significant contributions to previous studies which we have conducted on *Orcaella*. We thank Mr. Guido Parra for use of photographs and his unpublished information on appearance of *Orcaella heinsobni* from



northeastern Australia. We thank I. Baird, T. Jefferson, D. Krebs, N. Piwpong, P. Stacey, J. Wang, and WWF Philippines–Malampaya Sound Ecological Studies Project Staff, for their hard work in obtaining tissue samples. We are grateful to R. LeDuc and A. Dizon for review and support with the genetics analyses. F. Archer kindly provided the *S. coerulealba* sequences for analyses. We thank J. Mead for providing details on Gray's publications and C. Wallace for nomenclatural advice. We thank publishers of The Raffles Bulletin of Zoology for permission to reproduce figures from an article previously published in that journal. We also thank Adella Edwards for preparing the figures. Many thanks to Graham Ross, George Heinsohn, Tom Jefferson, Tom Evans, and two anonymous referees for reviewing earlier versions of the manuscript.

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Received: 27 April 2004

Accepted: 23 November 2004

Appendix 1. List of specimens examined for external morphometrics analyses. Australian specimens 1–4 and Asian specimens 27–38 were classified as juveniles and excluded from further analyses. The specimens in the “#” column with one asterisk “\*” were only included in the descriptive statistics. Those with two asterisks “\*\*” were also included in the multivariate analyses.

Identification number	#	Date	Location	Country	Sex	Weight	Total length	Reference
Australian specimens								
MM64	1	5-Aug-72	Pallarenda	Australia	Female	9.92 kg	91.00	Arnold and Heinsohn (1996)
—	2	—	Townsville	Australia	—	—	105.00	Arnold and Heinsohn (1996)
—	3	3-Mar-93	10 km South Pallarenda	Australia	—	24 kg	130.00	This paper
—	4	—	Townsville	Australia	—	—	134.00	Arnold and Heinsohn (1996)
—	5**	—	Townsville	Australia	—	—	186.00	Arnold and Heinsohn (1996)
—	6*	—	Townsville	Australia	—	—	187.00	Arnold and Heinsohn (1996)
CET1003	7*	30-Jul-76	Town Common, Townsville	Australia	—	—	211.00	Arnold and Heinsohn (1996)
—	8*	—	Townsville	Australia	—	—	212.00	This paper
MM81	9**	18-Aug-74	Pallarenda	Australia	Female	—	212.00	Arnold and Heinsohn (1996)
MM92	10*	24-Aug-75	Kissing Point, Townsville	Australia	Female	—	212.00	Arnold and Heinsohn (1996)
CET1004	11*	10-Sep-76	Rowes Bay, Townsville	Australia	Female	—	212.00	Arnold and Heinsohn (1996)
MM61	12**	21-Apr-72	Horseshoe Bay, Townsville	Australia	Male	114.4 kg	213.50	Arnold and Heinsohn (1996)
MM12	13**	23-Apr-70	Horseshoe Bay, Townsville	Australia	Male	—	215.00	Arnold and Heinsohn (1996)
MM30	14**	10-Jun-71	Pallarenda	Australia	Female	128 kg	215.00	Arnold and Heinsohn (1996)
MM54	15**	18-Mar-72	Kissing Point, Townsville	Australia	Male	—	215.00	Arnold and Heinsohn (1996)
MM63	16**	5-Aug-72	Pallarenda	Australia	Female	190 kg	217.00	Arnold and Heinsohn (1996)
—	17*	—	Townsville	Australia	—	—	219.00	Arnold and Heinsohn (1996)
MM13	18**	23-Apr-70	Horseshoe Bay, Townsville	Australia	Male	—	219.00	Arnold and Heinsohn (1996)
MM25	19**	23-Jan-71	Horseshoe Bay, Townsville	Australia	Female	—	220.00	Arnold and Heinsohn (1996)
MM82	20**	18-Aug-74	Pallarenda	Australia	Female	—	222.00	Arnold and Heinsohn (1996)
MMA	21*	11-Nov-68	Horseshoe Bay, Townsville	Australia	Female	—	225.00	This paper
MM32	22*	4-Sep-71	Kissing Point, Townsville	Australia	Female	133 kg	225.00	Arnold and Heinsohn (1996)
MM88	23**	28-Mar-75	Townsville	Australia	Female	—	225.00	Arnold and Heinsohn (1996)
MM16	24**	3-Oct-70	Pallarenda	Australia	Female	—	226.00	Arnold and Heinsohn (1996)
MM14	25**	23-Apr-70	Horseshoe Bay, Townsville	Australia	Male	—	235.00	Arnold and Heinsohn (1996)
CET1006	26*	4-Oct-76	Rowes Bay, Townsville	Australia	Male	—	270.00	This paper

Appendix 1. Continued.

Identification number	#	Date	Location	Country	Sex	Weight	Total length	Reference
Asian specimens								
OBRE3	27	16 July 1876	India	India	Female	10.45 kg	86.00	Anderson (1879)
OBRE04-22/03	28	22 Mar-04	Kratie Province, Mekong River	Cambodia	Female	10.8 kg	91.00	Beasley, unpublished
OBRE04-03/02	29	04-Feb-04	Kratie Province, Mekong River	Cambodia	Male	9.5 kg	94.00	Beasley, unpublished
OBRE04-24/02	30	24-Feb-04	Kratie Province, Mekong River	Cambodia	Male	12.5 kg	99.00	Beasley, unpublished
OBRE01-21/02	31	21-Feb-01	Songkhla Lake	Thailand	Male	10.1 kg	99.80	Beasley et al. (2002a)
MCB002	32	24-May-01	Malampaya Sound	Philippines	Male	16 kg	100.00	Smith et al. (2001) <sup>a</sup>
OBRE02-08/09	33	8-Sep-02	Kratie Province, Mekong River	Cambodia	Female	15.7 kg	106.30	Beasley et al. (2003) <sup>b</sup>
OBRE01-25/11	34	25-Nov-01	Kratie Province, Mekong River	Cambodia	Male	14.8 kg	107.00	Beasley et al. (2003)
OBRE02/02	35	1-Feb-00	Chilka Lake	India	—	—	107.30	Sinha et al., unpublished <sup>c</sup>
OBRE04-18/03	36	18-Mar-04	Kratie Province, Mekong River	Cambodia	Female	13.5 kg	113.00	Beasley, unpublished
OBRE04-20/03	37	20-Mar-04	Kratie Province, Mekong River	Cambodia	Male	13.9 kg	114.00	Beasley, unpublished
ISUI	38	21-Feb-80	Mahakam River	Indonesia	Female	—	153.00	Tas'an et al. (1980) <sup>d</sup>
OBRE04-08/02	39**	08-Feb-04	Kratie Province, Mekong River	Cambodia	Female	75.5 kg	173.00	Beasley, unpublished
MCB003	40*	22-Aug-01	Malampaya Sound	Philippines	Male	110 kg	176.00	Smith et al. (2001)
OBRE02-21/09	41*	21-Sep-02	Kratie Province, Mekong River	Cambodia	Male	82 kg	176.50	Beasley et al. (2003)
OBRE2	42**	16-Jul-1876	India	India	Female	—	180.00	Anderson (1879)
OBRE00-12/10	43**	12-Oct-00	Songkhla Lake	Thailand	Male	—	187.00	Beasley et al. (2002b)
OBRE04-13/03	44**	12-Mar-04	Kratie Province, Mekong River	Cambodia	Male	68 kg	188.00	Beasley, unpublished

Appendix 1. Continued.

Identification number	#	Date	Location	Country	Sex	Weight	Total length	Reference
OBRE95-04/05	45**	4-May-95	Songkhla Lake	Thailand	Male	64 kg	188.00	Beasley <i>et al.</i> (2002b)
LLOZE1	46**	—	Mekong River	Cambodia	Female	80 kg	190.00	Lloze (1973)
OBRE1973	47*	26-May-73	Songkhla Lake	Thailand	—	—	193.00	Pilliri and Gihir (1973–1974)
LLOZE2	48**	—	Mekong River	Cambodia	Female	87 kg	200.00	Lloze (1973)
OBRE1	49*	01-Jun-1876	India	India	Female	—	210.00	Anderson (1879)
OBRE01-18/04	50*	18-Apr-01	Songkhla Lake	Thailand	—	—	210.00	Beasley <i>et al.</i> (2002b)
SEMAYANG	51*	21-Feb-80	Mahakam River	Indonesia	Female	—	211.00	Tas'an <i>et al.</i> (1980)
OFLU2	52*	01-Jul-1876	Bhamoo	Myanmar	Male	—	219.00	Anderson (1879)
OBRE1903A	53*	17-Mar-05	Tanjong, Patani	Thailand	Male	—	220.00	Pilliri and Gihir (1973–1974)
MAHAKAM	54*	21-Feb-80	Mahakam River	Indonesia	Male	—	—	Tas'an <i>et al.</i> (1980)
OBRE03-22/12	55**	22-Dec-04	Kratie Province, Mekong River	Cambodia	Female	96.95 kg	228.00	Beasley, unpublished
OFLU1	56*	15-Mar-1870	Bhamoo	Myanmar	Male	—	229.00	Anderson (1879)
OBRE97-20/11	57**	20-Nov-97	Songkhla Lake	Thailand	—	98 kg	229.00	Beasley <i>et al.</i> (2002b)
OBRE1903B	58*	17-Mar-05	Tanjong, Patani	Thailand	Male	—	275.00	Pilliri and Gihir (1973–1974)
07.12.94	59	7-Dec-94	Chilika Lake	India	—	—	—	Sahu <i>et al.</i> 1998 <sup>e</sup>
31.01.95	60	31-Jan-95	Chilika Lake	India	—	—	—	Sahu <i>et al.</i> 1998

<sup>a</sup> Smith, B. D., I. Beasley and M. Buccat. 2001. Final report on the dolphin component of the Malampaya Sound ecological studies project. Unpublished report submitted to WWF Philippines, Manila.

<sup>b</sup> Beasley, I. L., P. Somany, S. Kin and Y. S. Sang. 2003. Mekong Dolphin Conservation Project: Status Report, July 2003. Unpublished report submitted to Wildlife Conservation Society, P. O. Box 1620, House 21, Street 21, Phnom Penh, Cambodia.

<sup>c</sup> Sinha, R. K., C. L. Trishal and A. K. Patnaik. Current status of the Irrawaddy dolphins (*Orcaella brevirostris*) in Chilika Lake, India and recommendations for conservation. Unpublished report submitted to the Chilika Development Authority, Orissa, India.

<sup>d</sup> Tas'an, A. Irwandy, Sumitro and S. Hendrokusumo. 1980. *Orcaella brevirostris* (Gray, 1866) from the Mahakam River. Unpublished report. Jaya Ancol Oceanarium, Jakarta.

<sup>e</sup> Sahu, H. K., S. K. Kar and S. K. Patnaik. 1998. Study of some aspects of Irrawaddy river dolphin *Orcaella brevirostris* (Gray) in Chilika Lake, Orissa. Indian Forester, October. 803–809.



Appendix 2. List of specimens examined for molecular analysis

SW/FSC lab no.	Field no.	Collection location	Collection date	Latitude and longitude	Tissue type
2905	#1	Australia–Northeast	1991	19°16'S, 146°48'E	Skin
2906	#2	Australia–Northeast	1993/03/03	19°16'S, 146°48'E	Skin
2907	#3	Australia–Holliday Bay	1993/05/20	21°10'S, 149°12'E	Skin
4006	PJS0001	Laos–Hang Khone, Mekong River	1993/05/15	13°56'S, 105°55'E	Skin
4007	PJS0002	Laos–Hang Khone, Mekong River	1993/05/17	13°56'S, 105°55'E	Skin
7203	95-1-LAO	Laos–Hang Sadam,	1995/03/18	15°07'S, 105°47'E	Skin
7204	95-2-LAO	Laos–Hang Khone, Mekong River	1995/03/26	13°56'S, 105°56'E	Skin
7205	95-3-LAO	Laos–Hang Khone, Mekong River	1995/03/26	13°56'S, 105°55'E	Skin
7206	96-1-LAO	Laos–Hang Khone, Mekong River	1996/05/15	13°56'S, 105°55'E	Skin
9258	IB92-01	Laos–Mekong River	1992/03	15°07'S, 105°47'E	Skin
9259	IB92-02	Laos–Mekong River	1992/03	15°07'S, 105°47'E	Skin
9260	IB92-03	Laos–Mekong River	1992/03	15°07'S, 105°47'E	Skin
9261	IB92-05	Thailand–Trat Province	1992/05/01	12°14'S, 102°30'E	Skin
14360	OB22/01/99	Indonesia–E. Kalimantan, Mahakam River	1999/01/22	0°30'S, 117°00'E	Skin
17365	ZZZ0067	Australia–Darwin	—	12°28'S, 130°50'E	Muscle
23962	OBRE01-21/01	Cambodia–Stung Treng	2001/01/21	13°31'S, 105°58'E	Skin
23963	OBRE01-23/01	Cambodia–Anlong Chiteal	2001/01/23	13°41'S, 106°00'E	Skin
23965	OBRE01-12/05	Cambodia–Tbong Klar	2000/12/05	13°15'S, 105°58'E	Skin
23969	OBRE01-21/02	Thailand–Songkhla Lake, Ko Yai Penn	2001/02/21	07°30'S, 100°16'E	Skin
23970	OBRE01-18/04	Thailand–Songkhla Lake, Lam Pam	2001/04/18	07°37'S, 100°09'E	Skin
23972	OBRE00-04/02	Thailand–Songkhla Lake, Ban Khoa Chan	2000/04/02	07°12'S, 100°36'E	Skin
23973	OBRE01-05/06	Thailand–Songkhla Lake, Klong Kud	2000/05/06	—	Skin
23974	OBRE94-12/08	Thailand–Songkhla Lake, Ban Samphao Nua,	1994/12/08	07°12'S, 100°36'E	Skin
23975	OBRE90-18/01	Thailand–Songkhla Lake, Ban Bak Sawa	1990/01/18	07°30'S, 100°05'E	Skin
23976	OBRE00-06/01	Thailand–Songkhla Lake, Ban Wae	2000/06/01	10°48'S, 119°26'E	Skin
31996	01MCB01-24/05	Philippines–New Guinlo, Malampaya Sound	2001/05/24	10°48'S, 119°26'E	Skin
31997	02MCB01-21/08	Philippines–Inner Sound, Malampaya Sound	2001/08/21	10°50'S, 119°24'E	Skin
31998	02MDM01-24/11	Philippines–New Guinlo, Malampaya Sound	2001/11/24	10°48'S, 119°26'E	Skin

## APPENDIX 3

*ORCAELLA BREVIROSTRIS* SPECIMENS EXAMINED

External morphometrics: 34 specimens from: Cambodia (13), India (6), Indonesia (3) Myanmar (Burma) (2), Philippines (2) and Thailand (8). Skull morphology: 77 specimens from: Bangladesh (1), Brunei (1), Cambodia (12), India (10), Indonesia (7), Malaysia (14), Myanmar (2), Singapore (2), Thailand (13), Vietnam (15). The cranial specimens from India included the type specimen of *O. brevirostris*; the Burmese (Myanmar) specimens were from the Ayeyarwady River and were identified as *O. fluminalis* by Anderson (1871). See Beasley *et al.* (2002b) for further details. DNA: 24 samples, from Cambodia/Laos (12), Indonesia (1), Philippines (3), Thailand (8); see Table 2 for further details.

## APPENDIX 4

*ORCAELLA BREVIROSTRIS* DESCRIBED AND FIGURED SPECIMENS

Figured and described specimens of *O. brevirostris* include Owen (in Gray 1866): fig. 57 (holotype skull); Owen (1866): plate 9, fig. 1–3 (holotype skull); Anderson (1879): plate 25 (external: coastal India); plate 25a (external: Ayeyarwady River system, Myanmar (Burma), and anatomy), plate 27–30 (anatomy), plate 33–38 (fetus and anatomy), plate 41 (internal casts of periotic bone), plate 42, 43 (skull and postcranial osteology); Kasuya (1973): p. 30, fig. 63, plate 11: 1–13 (tympano-periotic bones); Pilleri and Gahr (1973–1974): pp. 136–138, table 9, plate 22–27 (external, taxidermy specimen, skull, postcranial osteology); Lloze (1982): plate 1 (external, captured animals, Mekong River system, Cambodia), plate 2 (skull); Tas'an and Leatherwood (1984): fig. 3, 4 (external, captive dolphins, Mahakam River system, Indonesia); Marsh *et al.* (1989): fig. 4 (external, captive dolphins, Mahakam River system, Indonesia); Pilleri *et al.* (1989): fig. 9 (tympanic bone), table 5 (periotic bone); Martin (1990): unnumbered figure, p. 90 (external, captive dolphin); Baird *et al.* (1994): fig. 1 (surfacing dolphin, Mekong River system, Laos), fig. 4 (skull), fig. 3, 5–8 (external, stranded, Mekong River system, southern Laos); Arnold and Heinsohn (1996): fig. 14. (dorsal view of holotype skull); Stacey and Arnold (1999): fig. 1 (external, captive dolphins, Mahakam River system, Indonesia); Arnold (2002): fig. 1 (external, captive dolphins, coastal Thailand); Beasley *et al.* (2002a): fig. 7, fig. 10B, fig. 12B (skulls); Smith and Hobbs (2002): fig. 1 (surfacing dolphins, Ayeyarwady River system, Myanmar); Beasley *et al.* (2002b): fig. 1 (external, captive dolphin, coastal Thailand), fig. 7, 8 (external, stranded/net caught animals, Songkhla Lake, Thailand); Krieb (2002): fig. 2 (surfacing dolphins, Mahakam River system, Indonesia); Dolar *et al.* (2002): fig. 7 (surfacing animals, Malampaya Sound, Philippines); Reeves *et al.* (2003a): unnumbered figures, pp. 450–451 (surfacing animals, coastal Cambodia).

## APPENDIX 5

*ORCAELLA HEINSOHNI* SPECIMENS EXAMINED

External morphometrics: 26 specimens from central Queensland, Arnold and Heinsohn 1996; this paper, Table 1. Skull morphology: 37 specimens from Townsville region, Queensland (19°12'S, 146°46'E), one specimen from Brisbane

River, Queensland (27°32'S, 152°49'E), five specimens from Northern Territory (12°00'S, 131°00'E), two specimens from Western Australia (17°57'S, 122°14'E), and one specimen from Daru, Papua New Guinea (8°45'S, 143°24'E): see Beasley *et al.* (2002a), appendix 1 for more details. DNA: three specimens from central Queensland, one from Northern Territory, this paper, Table 2.

## APPENDIX 6

## ORCAELLA HEINSOHNI DESCRIBED AND FIGURED SPECIMENS

*O. brevirostris* Johnson (1964), pp. 502–505, plate 14,15; Dawbin (1972): 272–274 (in part), unnumbered figure, p. 273; Mitchell (1975): fig. 12, 42; Leatherwood and Reeves (1983): unnumbered figures, pp. 152, 154; Marsh (1984): unnumbered figure, p. 300; Marsh *et al.* (1989) (in part), table 1 (Townsville data), table 2 (Townsville data), fig. 3 (skull); Arnold and Heinsohn (1996) (in part): descriptions, pp. 145–150, 158–160, 168–170, table 1–3 and 6, appendix table 1, fig. 2–13, 15–36, 48–57; Stacey and Arnold (1999): fig. 2, 3 ; Beasley *et al.* (2002a) (all references to specimens from Australia and Papua New Guinea, fig. 7 (above), fig. 10A, fig. 12A).

*Appendix 7.* External, skeletal and molecular diagnostic features of *Orcaella* species. Within each category, features that are most likely to differentiate an individual specimen are listed first. For features with one asterisk "\*" differences were statistically highly significant and showed minimal range overlap; format of values is mean  $\pm$  SD, with range and sample size in parentheses.

Feature	<i>Orcaella heinsobni</i>	<i>Orcaella brevirostris</i>
External		
*dorsal fin height	4.4 % $\pm$ 0.57 (3.4–5.3, $n = 16$ )	3.0 % $\pm$ 0.50 (2.1–4.0, $n = 18$ )
dorsal groove	absent	present (Fig. 5a, b)
color pattern	tripartite, with dorsal cape (Fig. 2c, d)	two-tone (Fig. 2a, b)
neck crease	generally well-developed	present, but often indistinct
Skeletal		
*number of nasal bones/ossicles	3.0 $\pm$ 1.77 nasals (0–6, $n = 37$ ) (Fig. 6a)	2.0 $\pm$ 0.14 (2–3, $n = 54$ ) (Fig. 6b)
*average nasal bone/ossicle width (mm)	9.3 $\pm$ 1.72 (5.8–13.2, $n = 26$ )	16.0 $\pm$ 2.83 (10.5–21.1, $n = 43$ )
*height of temporal fossa (mm)	61.2 $\pm$ 5.55 (49.1–83.2, $n = 41$ ) (Fig. 7, above)	45.8 $\pm$ 4.19 (33.0–55.3, $n = 53$ ) (Fig. 7, below)
*length of antorbital process (mm)	38.6 $\pm$ 3.63 (31.8–53.2, $n = 40$ )	26.3 $\pm$ 3.82 (17.0–32.6, $n = 50$ )
*depth of pterygoid notch (mm)	24.5 $\pm$ 2.91 (19.4–31.2, $n = 31$ )	38.1 $\pm$ 4.45 (30.7–48.6, $n = 33$ )
*minimum distance between pterygoid hamuli (mm)	4.0 $\pm$ 1.81 (1.6–9.8, $n = 32$ ) (Fig. 8a)	14.5 $\pm$ 2.78 (7.9–20.7, $n = 38$ ) (Fig. 8b)

## Appendix 7. Continued.

Feature	<i>Orcaella heinsobni</i>	<i>Orcaella brevirostris</i>
mesethmoid plate	reduced, rarely reaching level of anteriormost nasal bones/ossicles ( $n = 44$ ) (Fig. 6a)	extensive, extending to level with or behind anteriormost point of nasal bones/ossicles ( $n = 55$ ) (Fig. 6b)
frontal bone exposure anterior to nasal bones	extensive ( $n = 44$ ) (Fig. 6a)	reduced or absent ( $n = 55$ ) (Fig. 6b)
supernumary bone	may be present ( $n = 44$ ) (Fig. 6a)	absent ( $n = 55$ ) (Fig. 6b)
vertebral count <sup>a</sup>	58–61 ( $n = 6$ )	62–63 ( $n = 4$ )
scapula <sup>a</sup>	acromion process usually larger than coracoid process	acromion process usually smaller than coracoid process
sternum <sup>a</sup>	compound	completely fused
Molecular		
control region D-loop	5.9% base pair difference ( $n = 4$ )	5.9% base pair difference ( $n = 24$ )
base pair differences	16 fixed base pair differences (one insertion/deletion, two transversions and 13 transitions) ( $n = 4$ )	16 fixed base pair differences (one insertion/deletion, two transversions and 13 transitions) ( $n = 24$ )

<sup>a</sup> Potentially of taxonomic significance, however limited by small sample size ( $<5$ ).