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SPINNER DOLPHINS (*STENELLA LONGIROSTRIS*) OF THE WESTERN PACIFIC AND SOUTHEAST ASIA: PELAGIC AND SHALLOW-WATER FORMS[1]

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ABSTRACT

A dwarf form of the spinner dolphin has been reported from the Gulf of Thailand, while more typical large spinner dolphins have been described from Japanese waters and other localities in the western Pacific. These reports have been based on very few specimens. Our purpose in this study was to determine the affinities of spinner dolphins throughout the region based on larger samples and to review their taxonomic status, with an hypothesis of two widespread ecotypic forms, or subspecies. We examined 213 osteological specimens, from a tuna gillnet fishery in the Philippines, from the former Taiwanese shark gillnet fishery in the Timor and Arafura Seas off northern Australia, from the Gulf of Thailand, from other areas in the western Pacific and Southeast Asia, from the eastern Indian Ocean, and from the Central and South Pacific. Results show that spinner dolphins from the deep inner waters of the Philippines conform to the large pelagic type of spinner dolphin that inhabits the Central and South Pacific, the western Pacific and the eastern Indian Ocean. The skull is similar in size and shape to the holotype specimen of *S. longirostris* (from unknown locality). This form feeds primarily on small mesopelagic fishes and squids. Spinner dolphins from the shallow waters of

[1] This paper is dedicated to Kenneth S. Norris, in commemoration of happy and productive times in California, Hawaii and the eastern tropical Pacific. He was a mentor to us all.

inner Southeast Asia represented in the sample, including the Gulf of Thailand, Timor Sea and Arafura Sea, are smaller in body and skull size, have fewer teeth and vertebrae, and feed mainly on benthic and coral reef fishes and invertebrates. We hypothesize that this form also inhabits the Java Sea and other shallow waters throughout inner Indonesia and Malaysia. We redescribe a subspecies corresponding to the small form and based on *Delphinus roseiventris* Wagner 1846 from the Arafura Sea, designating a neotype and paraneotype specimens.

Key words: *Stenella longirostris, Delphinus roseiventris,* spinner dolphin, taxonomy, morphology, subspecies, geographical variation, feeding habits, Southeast Asia, Australia, Philippines.

The spinner dolphin occurs around the world in the tropics and is generally considered to be a pelagic species inhabiting deep water and feeding mainly on mesopelagic fishes and squids (Perrin and Gilpatrick 1994). However, a dwarf form has been reported from the very shallow (<50 m) Gulf of Thailand (Perrin *et al.* 1989), based on 10 specimens caught incidentally in shrimp trawls. It is similar in size to spinner dolphins caught in shark gillnets in the shallow Arafura and Timor Seas off northern Australia. The stomachs of the Australian spinners contained benthic and reef-dwelling organisms rather than mesopelagic species. The purpose of the present study was to determine the affinities of spinner dolphins throughout the region based on larger samples and to review their taxonomic status, with an hypothesis of two widespread ecotypic forms, or subspecies

Methods and Materials

The study area included the Central Pacific, South Pacific, Western Pacific, Southeast Asia and the far western Indian Ocean. We examined 213 osteological specimens from the region (Appendix 1). The majority were from fishery by-catches: 10 from the shrimp trawl fishery in Thailand, 37 from a former Taiwanese shark gillnet fishery off northern Australia in the Timor and Arafura Seas (Harwood and Hembree 1987), 74 from a tuna driftnet fishery operating out of Siaton in Negros Oriental in the Philippines (Dolar 1994), 21 from directed fisheries (Pamilacan Island in Bohol and Selinog Island in Mindanao in the Philippines [Dolar *et al.* 1994], Japan and Indonesia), 14 from strandings, and 57 from other sources (live-capture, at-sea collections, unknown sources). In addition, we had total length and sex for the majority of the specimens and for others from off Australia for which the skulls were not collected; total length and (in some cases) sex for additional specimens from Thailand (Anderson and Kinze 1995); other external measurements for most of the Thai, Australian, and Philippine series; data on sexual maturity for most of the Philippine specimens and some of the Australian specimens; and data on stomach contents (otoliths, cephalopod beaks, and semidigested remains of fish, cephalopods, and crustaceans) for Australian and Philippine specimens.

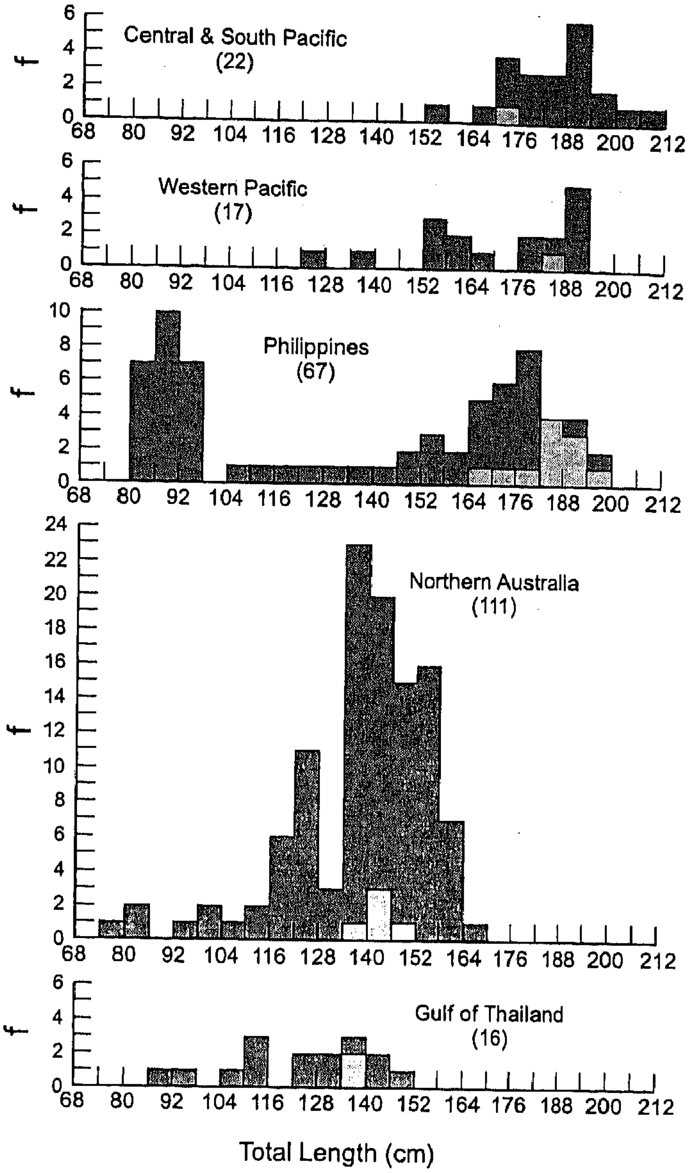

Figure 1. Body length of spinner dolphins from five regions. Less-dense shading represents specimens known to be physically mature. Sample size in parentheses.

Skull measurements were as described in Perrin (1975), taken to the nearest mm. Specimens were judged cranially adult in which the maxillae and premaxillae were fused distally (Perrin and Heyning 1993). Specimens with all vertebral epiphyses fused to the centra were considered physically mature. The number of vertebrae in specimens missing the terminal 1–3 vertebrae was estimated by comparison with intact specimens. The number of teeth was determined by counting alveoli. In the analyses, lowest and highest lower and upper counts were used, with a single upper or lower count taken as an estimate. External measurements followed Norris (1961). For the Philippine specimens, long measurements (*e.g.*, body length and tip of beak to umbilicus) were taken to the nearest cm and shorter measurements to the nearest mm.

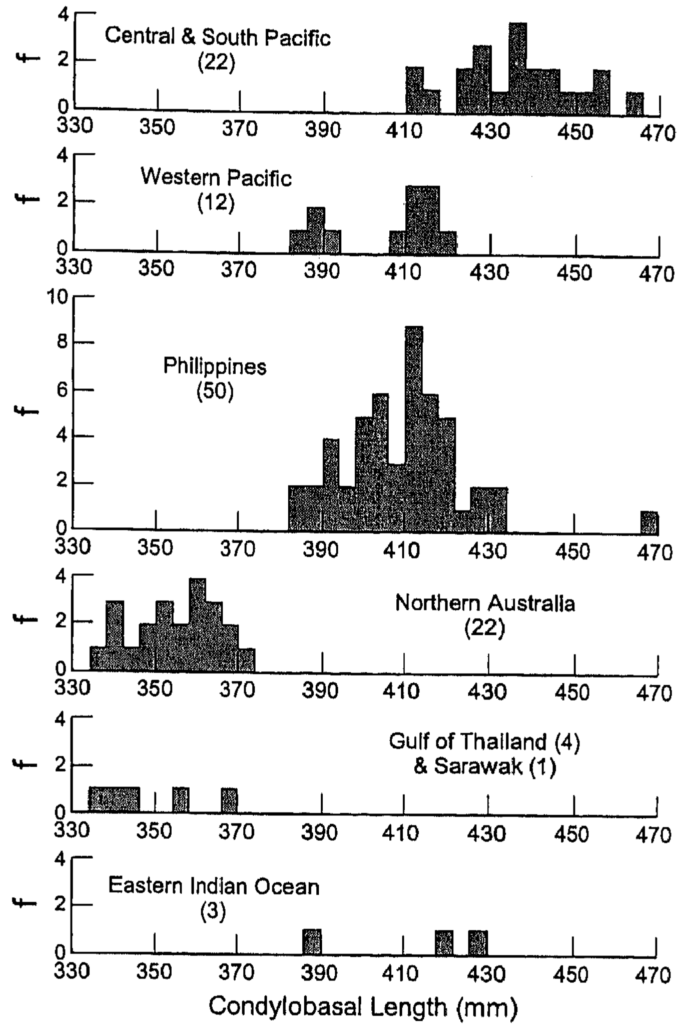

Figure 2. Skull length of spinner dolphins from six regions. Sample size in parentheses.

Measurements of the Australian specimens were usually to the nearest 0.5 cm, although this could not always be determined from the raw data sheets. These varying degrees of precision are reflected in the table below of external measurements.

In our experience, some of the variation in external measurements between series measured by different investigators is ascribable to slight differences in how the measurements were taken (instrument used, position of the animal, and interpretation of the measurement by the observer). The Philippine specimens were measured by WFP, MLLD, and assistants; the Australian specimens were measured by a number of different investigators aboard fishing vessels and at an oceanarium. This should be kept in mind when considering variances of the measurements and differences between the series in the data given here, especially in the case of values at the extremes of the ranges of the measurements. All osteological measurements were taken by WFP, except for those of

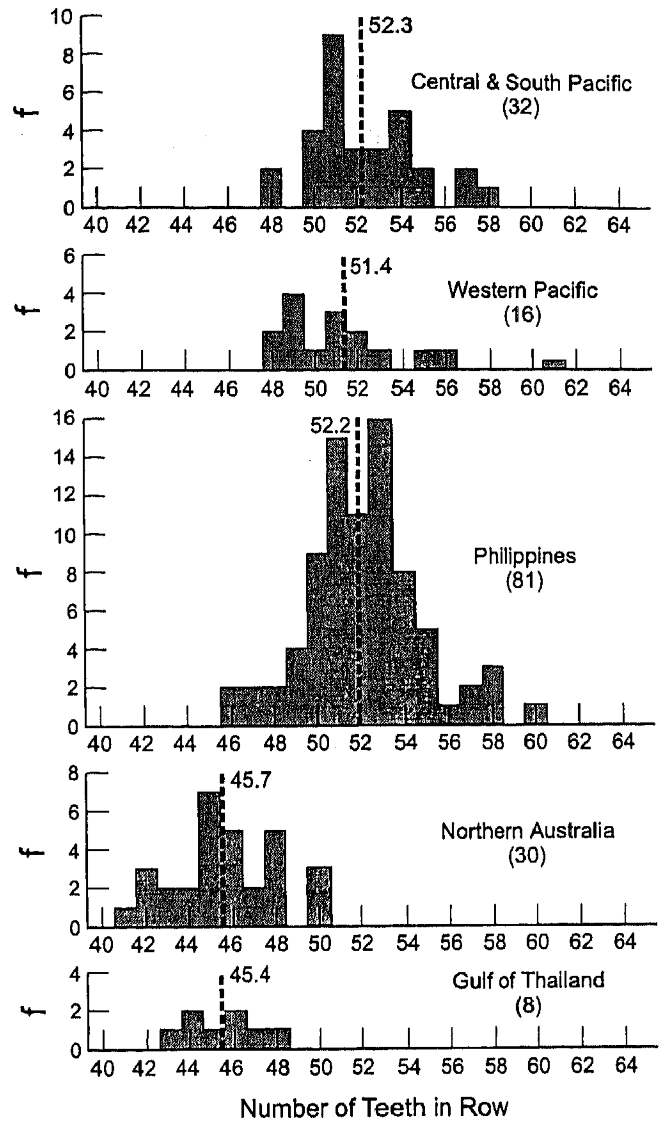

Figure 3. Average and frequency distribution of number of teeth in lower toothrow (highest of left and right) in spinner dolphins from five regions. Sample size in parentheses.

the specimens in the Paris Museum, which were taken by DR; missing values for specimen MNHN A-3026 were taken from True (1889).

Sample sizes, sex ratios and distributions of body size for the northern Australian samples are slightly different than those presented by Hembree (1986) and Perrin *et al.* (1989); this reflects resolution of problems of specimen identification in the raw data.

Discriminant analysis was carried out using the statistical software package SYSTAT 8.0 (SPSS, Inc. 1998), with default settings. Variables and specimens with missing values were excluded from the analysis. Other analyses were accomplished with MS EXCEL 7.0 (Microsoft 1996).

Acronyms for museums and other collections are defined in Appendix 2.

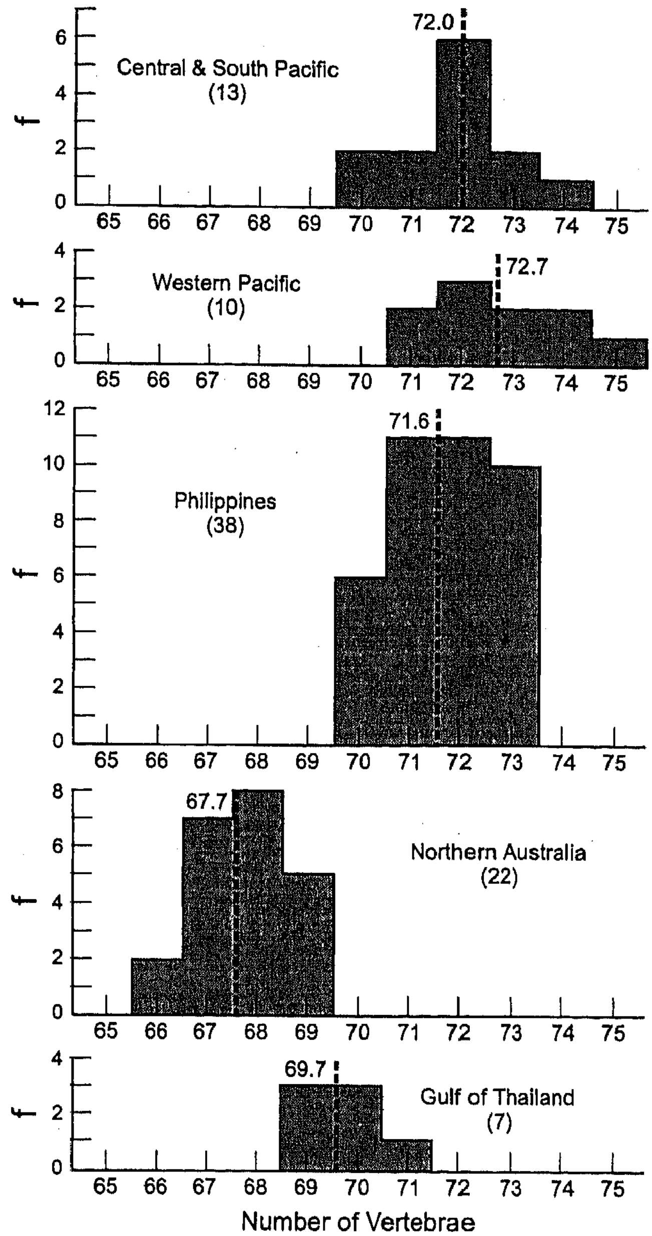

Figure 4. Average and frequency distribution of number of vertebrae in spinner dolphins from five regions. Sample size in parentheses.

Results

Morphology

Comparison of five geographical series in length of body, length of skull, number of teeth and number of vertebrae (Fig. 1–4) shows close affinities between the Gulf of Thailand, Sarawak and northern Australian specimens on one hand, indicating existence of a small form with relatively low tooth and vertebra counts in these areas, and the Philippine, Western Pacific, and Central and South Pacific specimens on the other. Adult length (Fig. 1) was about

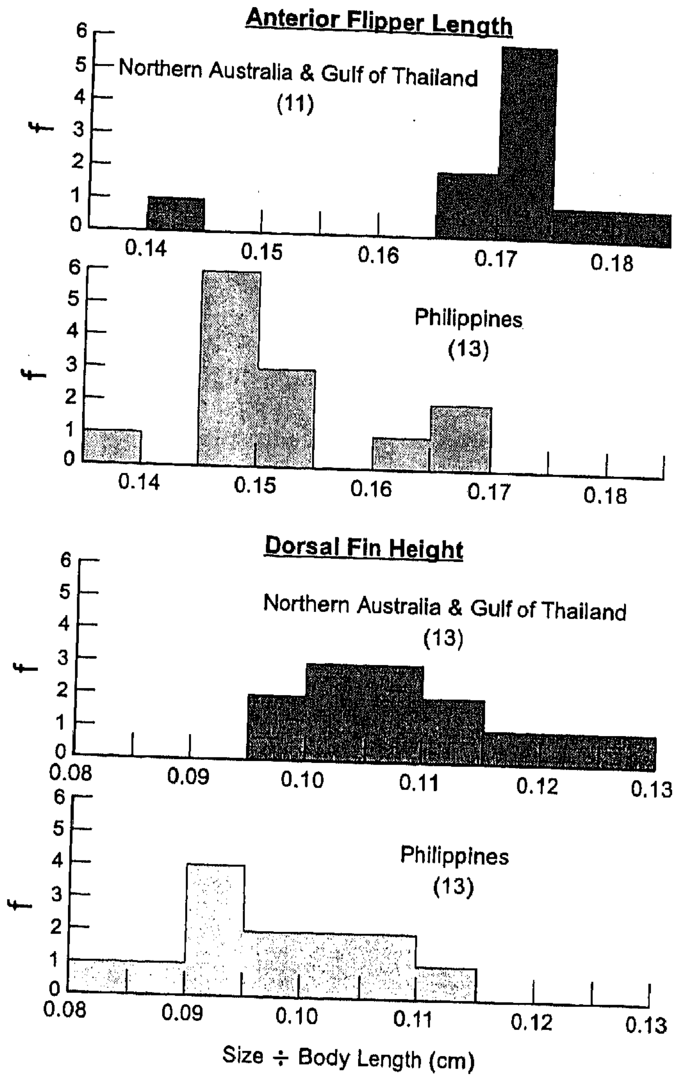

Figure 5. Size of flipper and dorsal fin relative to body size in cranially mature adults of small form (northern Australia and Gulf of Thailand) and large form (Philippines) of spinner dolphin in Southeast Asia. Sample size in parentheses.

30–40 cm less in the Thai and northern Australian dolphins than in those from the other areas. Adult skull length (Fig. 2) was about 50–60 mm less in the Thai, Sarawak and northern Australian specimens than in the Philippine and Western Pacific specimens and even less than in spinners from farther east in the Central and South Pacific. Three skulls from the eastern Indian Ocean grouped with the larger skulls; thus the small spinner is sandwiched between larger spinners to the east and to the west. The average highest tooth count in the lower tooth row (Fig. 3) was 45–46 in the Thai and northern Australian series *vs.* 51–53 in the Central and South Pacific, Western Pacific and Philippines, a difference on the average of about five teeth, or about 20 for all four tooth rows. Vertebral count (Fig. 4) was 2–4 lower in the Thai and northern Australian series than in those from the Central and South Pacific,

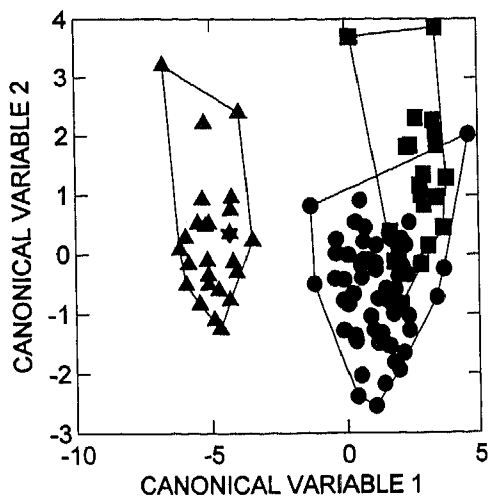

Figure 6. Discriminant analysis of three geographic series of spinner dolphins from Southeast Asia, based on osteological characters. Triangles = *S. l. roseiventris,* circles = *S. l. longirostris* from western Pacific, squares = *S. l. longirostris* from Central and South Pacific. Star = neotype specimen of *S. l. roseiventris.*

Western Pacific and Philippines, although the pattern is less clear in this case; the average for the small sample of Thai specimens fell between those for northern Australia and the Philippines.

While the sample sizes are very small, and comparison of external-mea-

Table 1. Canonical discriminant functions—standardized by within variance.

Function constant	1 −36.649	2 −0.573
Condylobasal length	0.024	0.064
Rostrum length	0.012	0.095
Rostrum width at base	−0.017	−0.114
Rostrum width at ¾ length	0.064	0.140
Rostrum width at ½ length	−0.065	0.149
Pmx width at ½ length	−0.062	−0.224
Tip of rostrum to external nares	0.026	0.034
Preorbital width	0.101	0.045
Postorbital width	0.066	−0.039
Zygomatic width	−0.059	0.259
Width of external nares	0.023	−0.009
Maximum width of premaxillae	−0.013	0.014
Parietal width	0.114	−0.123
Height of temporal fossa	−0.147	0.131
Length of orbit	−0.040	0.164
Length of upper toothrow	−0.031	−0.033
Highest lower toothcount	0.159	−0.204
Length of ramus	−0.006	−0.122
Height of ramus	−0.045	0.077

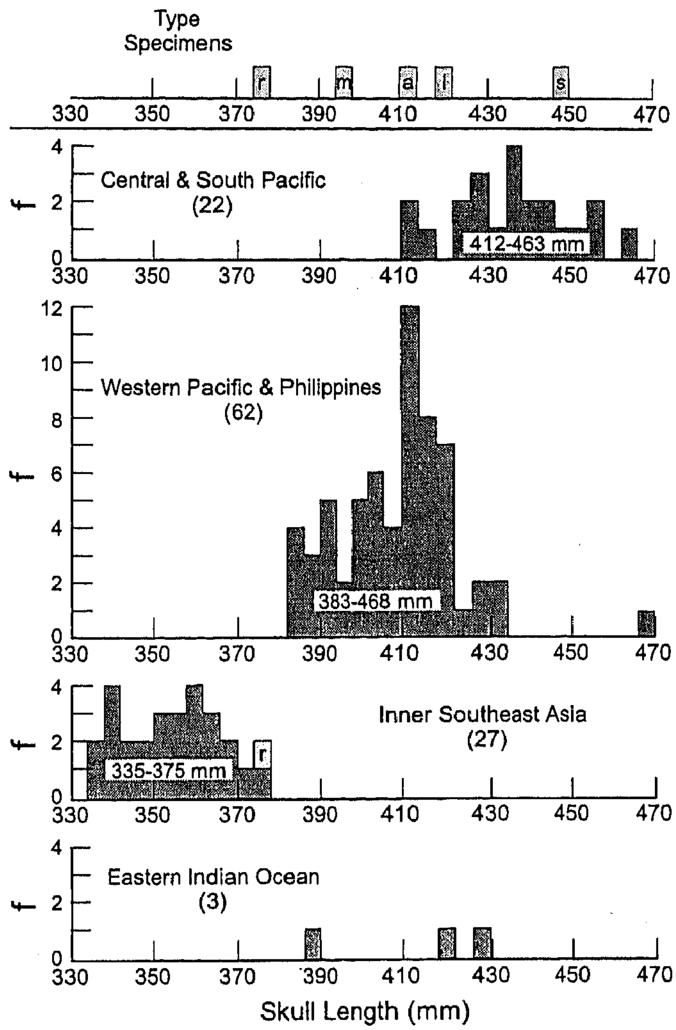

Figure 7. Frequency distribution of adult skull length for four geographical series of spinner dolphins. Type specimens for five nominal species in synonymy of *Stenella longirostris* at top: *r* = *Delphinus roseiventris* Wagner, 1846; *m* = *D. microps* Gray, 1846; *a* = *D. alope* Gray, 1846; *l* = *D. longirostris* Gray, 1828; *s* = *D. stenorhynchus* Gray, 1866.

surement data taken by different investigators can only be done with caution (see Methods and Materials), it appears that proportionate size of the flippers and dorsal fin was greater in the dolphins from Thailand and northern Australia than in those from the Philippines (Fig. 5).

A discriminant analysis of osteological measurements and tooth counts of specimens in three groups (Thailand and northern Australia combined, Philippines and western Pacific combined, and Central and South Pacific; Fig. 6 and Table 1) arrived at 100% correct classification of the small form using lower tooth count and 18 cranial measurements. Specimens were correctly classified to the other two series 91% and 82% of the time, respectively; none were classified with the small form.

Table 2. Selected external measurements (in cm) and weights (in kg) for *Stenella longirostris roseiventris* and series of *S. l. longirostris* from western Pacific (Philippines). Means, standard deviations (for sample sizes ≥5), sample size (in parentheses), and minimum and maximum values given for physically mature specimens; only minimum and maximum values and sample size given for cranially mature and sexually mature specimens (may be still growing in postcranial dimensions). See Appendix 1 for specimens included and text for details of methods and precision.

	S. l. roseiventris	*S. l. longirostris*
Body length		
Males:		
cranially mature	(17) 129–158	(21) 165–194
sexually mature	(3) 133–137	(15) 160–194
physically mature	144.8 ± 7.88	186.7 ± 4.23
	(8) 135–158	(6) 181–191
Females:		
cranially mature	(5) 138–145	(15) 139–195
sexually mature	—	(10) 147–195
physically mature	—	180.0 ± 10.95
	(1) 145	(5) 167–195
Weight		
Males:		
cranially mature	(10) 21.5–36.0	(13) 40.5–70.5
sexually mature	(3) 21.5–26.5	(10) 54.5–70.5
physically mature	30.3 ± 5.13	64.20 ± 3.944
	(5) 26–36	(5) 60.5–70.5
Females:		
cranially mature	(4) 26.0–31.0	(7) 45.5–63.2
sexually mature	—	(8) 34.1–63.2
physically mature	—	53.18 ± 8.216
	(1) 31.0	(5) 45.5–63.2
Tip of beak to anus		
Males:		
cranially mature	(8) 107–117	(15) 117–141
sexually mature	—	(11) 117–141
physically mature	113.0	134.0 ± 2.00
	(3) 110–117	(5) 132–137
Females:		
cranially mature	(3) 101–108	(9) 100–144
sexually mature	—	(8) 108–144
physically mature	—	132.6 ± 7.02
	—	(5) 127–144
Tip of beak to umbilicus		
Males:		
cranially mature	(8) 69–80	(15) 78.5–94
sexually mature	—	(11) 78.5–94
physically mature	73.0	91.0 ± 1.00
	(3) 70–75	(5) 90–92
Females:		
cranially mature	(3) 72–74	(9) 73.0–99
sexually mature	—	(8) 76–99
physically mature	—	91.2 ± 5.81
	—	(5) 85–99

Table 2. Continued.

	S. l. roseiventris	*S. l. longirostris*
Tip of beak to origin of flipper		
Males:		
cranially mature	(8) 37.5–44.0	(15) 39–46
sexually mature	—	(11) 39–47
physically mature	40.00 (3) 39.0–41.0	44.6 ± 0.89 (5) 44–46
Females:		
cranially mature	(3) 39.0–41.0	(8) 38–52
sexually mature	—	(7) 41–52
physically mature	— —	46.2 ± 4.32 (5) 41–52
Tip of beak to center of eye		
Males:		
cranially mature	(8) 25.5–31.0	(15) 27.5–31.4
sexually mature	—	(11) 27.5–33.1
physically mature	27.83 (3) 26.5–29.0	30.36 ± 0.270 (5) 30.1–30.8
Females:		
cranially mature	(3) 28.0–30.0	(9) 25.6–34.6
sexually mature	—	(7) 29.5–34.6
physically mature	— —	32.12 ± 2.18 (5) 29.5–34.6
Anterior length of flipper		
Males:		
cranially mature	(8) 23.0–27.0	(15) 24.1–29.4
sexually mature	—	(11) 24.1–29.4
physically mature	26.00 (3) 25.0–27.0	28.18 ± 0.610 (5) 27.9–29.2
Females:		
cranially mature	(3) 23.0–24.0	(8) 24.7–27.7
sexually mature	—	(7) 22.3–27.7
physically mature	— —	19.70 ± 1.628 (5) 17.2–21.6
Maximum width of flipper		
Males:		
cranially mature	(8) 8.0–10.0	(14) 8.7–12.5
sexually mature	—	(10) 8.7–10.1
physically mature	9.33 (3) 9.0–10.0	9.70 ± 0.200 (5) 9.6–10.0
Females:		
cranially mature	(2) 9.0	(8) 8.0–10.5
sexually mature	—	(7) 7.6–10.5
physically mature	— —	9.16 ± 0.783 (5) 8.1–10.0
Maximum span of flukes		
Males:		
cranially mature	(8) 34.5–40.5	(14) 32.4–48.8
sexually mature	—	(11) 36.2–48.8
physically mature	35.83 (3) 34.0–38.0	45.04 ± 3.906 (5) 41.2–48.8

Table 2. Continued.

	S. l. roseiventris	*S. l. longirostris*
Females:		
cranially mature	(2) 31.0–36.0	(8) 33.0–44.4
sexually mature	—	(7) 28.2–44.4
physically mature	—	40.40 ± 2.973
	—	(5) 37.8–44.4
Height of dorsal fin		
Males:		
cranially mature	(8) 14.5–17.5	(15) 13.8–20.5
sexually mature	—	(11) 16.0–20.5
physically mature	15.17	18.98 ± 1.497
	(3) 14.5–16.0	(5) 18.6–20.5
Females:		
cranially mature	(3) 13.0–15.0	(7) 14.0–18.6
sexually mature	—	(7) 10.9–18.6
physically mature	—	16.56 ± 1.210
	—	(5) 15.6–18.6

Feeding Habits

The stomachs of the Philippine dolphins (n = 49) contained mostly mesopelagic and deep-living benthic fishes (Argentinidae, Bregmacerotidae, Diretmidae, Gempylidae, Gonostomatidae, Macrouridae, Melamphiidae, Myctophidae, Neoscopelidae, Nomeidae, Paralepidae, Percichthyidae, Scomberososcidae, Scopelarchidae, Sparidae, and Trichuridae), mesopelagic squids (Brachioteuthidae, Chiroteuthidae, Cranchiidae, Enoploteuthidae, Histioteuthidae, Octopodoteuthidae, and Ommastrephidae) and shrimps of the families Onoplophoridae, Penaeidae and Sergestidae (species listed in Dolar, 1999). The northern Australian dolphins (n = 6) contained mostly shallow-water benthic and reef-dwelling fishes (Apogonidae [*Apogon* sp.], Bregmacerotidae [*Bregmaceros maclellandi*], Carangidae [*Selar boops, Decapterus* sp., *Megalaspis cordyla, Leiognathus* cf *L. berbis*], Congridae [*Uroconger lepturus*], Monocanthidae [*Paramonocanthus filicauda*], Muraenidae [*Gymnothorax* sp.] and Ophichthidae [*Muranichthys* sp.]) and unidentified squid, cuttlefish and shrimp (Hembree 1986; Hembree, unpublished data[2]).

Discussion and Conclusions

We conclude that spinner dolphins in the Philippines are of the same ecological and morphological form as those in the western, Central and South Pacific—large, pelagic, and feeding mainly on mesopelagic fishes and squids. They are referable to *Stenella longirostris longirostris* (Gray, 1828) on the basis of skull size (Perrin 1990). Spinner dolphins in shallow waters of inner South-

[2] Archived as "Catalogue of cetacean data sets (Durant Hembree and Australian Observer Program)" at Australian Nature Conservation Agency, Canberra, Australia.

east Asia not facing major oceans or seas (in Thailand, Indonesia, Malaysia, and northern Australia) on average are smaller and have fewer vertebrae, smaller skulls, and fewer teeth than the parapatric large pelagic form; they feed on benthic and reef-dwelling organisms. We conclude that they are distinct from other spinner dolphins at the specific level at least.

The nominal species *Delphinus roseiventris* Wagner,1846 was based on material collected by the *Astrolabe & Zélée* expedition in 1839 in the northern Arafura Sea (in a region included in what was then called *mer des Moluques*—the Moluccan Sea is now considered to be only the area roughly between Halmahera and Sulawesi/Celebes, considerably to the northwest of the Arafura Sea) (Jacquinot 1844, 1846).[3] Several specimens from the collection in the Arafura Sea are presently in the National Museum of Natural History (MNHN) in Paris; they conform to the small type of spinner dolphin from inner Southeast Asia as described above (Fig. 6, 7), and we therefore apply the name to the subspecies.

The nomenclatural history of *D. roseiventris* is anomalous. Sometime between 1842 and 1846, Jacquinot published an atlas of the *Astrolabe & Zélée* expedition in parts, including plates of the external appearance and skull of the "*dauphin à ventre rose.*" Wagner (1846) duplicated the plate of external appearance in a semi-popular compilation. He translated the name on the plate into Latin, as *Delphinus roseiventris,* but with no mention of the plate in the text or in the list of plates. The full report of the expedition appeared in 1853 (Jacquinot and Pucheran 1853), with the previously published plates and a full description of the species, including reference to "three skulls" and acknowledgment of Wagner's binomial. Three skulls, two disassociated postcranial skeletons and a mounted specimen from the expedition are in the MNHN. The mounted specimen is not the specimen illustrated by Jacquinot (and Wagner); it is too small (Robineau 1990), and it is not possible to determine whether one of the three skulls and/or the two skeletons came from the illustrated specimen (Robineau 1990). Given this situation, Robineau (1990) designated one of the expedition skulls (MNHN A-3026) as a lectotype and the

[3] The Paris osteological material consists of three skulls (A-3026, A-3027 and 1928-192) and two postcranial skeletons (1880-554 and 1880-553) which cannot be assigned unambiguously to the skulls. Old catalogs in the Museum note specimen A-3027 as taken on 4 March 1839 and specimen 1928-192 on 23 March 1839. Textual references in Jacquinot (1844) place the expedition on those dates in the coastal waters of New Guinea at about 135°E in the northern Arafura Sea and in the Arafura Sea between Cape Valsch (False Cape, *Tg. Vals*) in Indonesian New Guinea (Irian Jaya) and Australia, respectively. The situation is not as clear for the third specimen, A-3026, which is cataloged only as "*mer de Moluques, Astrolabe 1840,*" without a precise date. The account of the voyage (Jacquinot 1846) makes no mention of capture of a dolphin while in the Arafura Sea in 1840. Thus it is most likely that the specimen was collected together with the others, in 1839 and that the catalog entry was only meant to associate it with the expeditions. Museum catalogs consulted at MNHN and specimen numbers applied to A-3026 and A-3027: *CAC, Catalogues des Collections d'Anatomie comparée* (A.3026, A.3027); *CAG, Catalogue des anciennes galeries d'Anatomie comparée* (BII/87, BII/108); *JAC, Journal du Laboratoire d'Anatomie comparée* (1880-553, 1880-554, 1928-192); *CGZ, Catalogue de la galerie de Zoologie (mammifères marines)* (no. 19).

Table 3. Means, standard deviations (for sample sizes ≥5), sample sizes (in parentheses) and maximum and minimum values for selected meristic characters for series of *Stenella longirostris longirostris* from western Pacific and Central/South Pacific and of *Stenella longirostris roseiventris.* See Appendix 1 for list of specimens included.

	S. l. longirostris		*S. l. roseiventris* (Inner Southeast Asia)
	Western Pacific	Central/ South Pacific	
Highest upper toothcount	53.6 ± 3.02 (82) 47–62	55.3 ± 3.27 (31) 51–62	46.5 ± 2.13 (35) 42–52
Highest lower toothcount	52.0 ± 2.80 (97) 46–61	52.3 ± 2.42 (32) 48–58	45.7 ± 2.31 (41) 41–50
Number of lumbar vertebrae	17.0 ± 0.82 (7) 16–18	17.7 (3) 16–19	17.0 ± 0.88 (23) 16–19
Number of caudal vertebrae	34.6 ± 2.07 (5) 33–38	32.7 (3) 32–34	30.1 ± 0.97 (19) 28–32
Total number of vertebrae	71.9 ± 1.18 (48) 70–75	72.0 ± 1.00 (13) 70–74	68.2 ± 1.24 (29) 66–71
First vertebra with vertical foramen	48.6 ± 1.48 (42) 48–52	48.2 ± 1.05 (14) 47–50	45.1 ± 1.67 (33) 41–48
Last vertebra with lateral process	55.0 ± 1.04 (41) 52–57	55.1 ± 0.53 (14) 54–56	52.0 ± 1.28 (32) 49–57
Last vertebra with neural process	60.0 ± 1.15 (33) 57–62	60.1 ± 0.95 (14) 59–61	57.3 ± 1.34 (31) 53–60
First vertebra with chevron bone	39.0 (4) 35–41	40.7 (3) 40–41	38.8 ± 0.80 (23) 38–40
Widest vertebra	23.8 ± 1.13 (39) 20–25	23.8 ± 1.47 (6) 21–25	23.3 ± 0.75 (23) 22–25
No. of vertebral ribs (highest of l. & r.)	15.1 ± 0.57 (46) 14–16	14.8 ± 0.44 (13) 14–15	13.8 ± 0.45 (35) 13–15
No. of sternal ribs (highest of l. & r.)	9.0 ± 0.47 (42) 8–10	9.0 ± 0.58 (13) 8–10	8.0 ± 0.59 (33) 7–9

others and the mounted specimen as paralectotypes, based on the fact that they were a series considered by Jacquinot when describing the species (*dauphin à ventre rose*), in other words, syntypes. However, under the technical requirements of the International Code of Zoological Nomenclature (International Trust for Zoological Nomenclature 1985), because Wagner (1846) first published the Latin binomial name *Delphinus roseiventris,* he is the describer of record of the species, the specimen shown externally in his plate (taken from Jacquinot) is the holotype, and there are no syntypes (other specimens mentioned or shown by Wagner). In summary, the holotype is lost or cannot be identified,[4] there are no (legal) syntypes, and thus (as noted by Rudolph *et al.* 1997) there is no basis for designating a lectotype. In this situation, a

[4] Perrin (1990) stated that the "probable" holotype specimen of *D. roseiventris* was "MNNH 1882-104 . . . a small skull . . . from the Muluccas?" (noted by Rudolph *et al.* 1997). This was an error; that specimen is from an unknown locality and is not associated with the Astrolabe and Zéléé Expeditions.

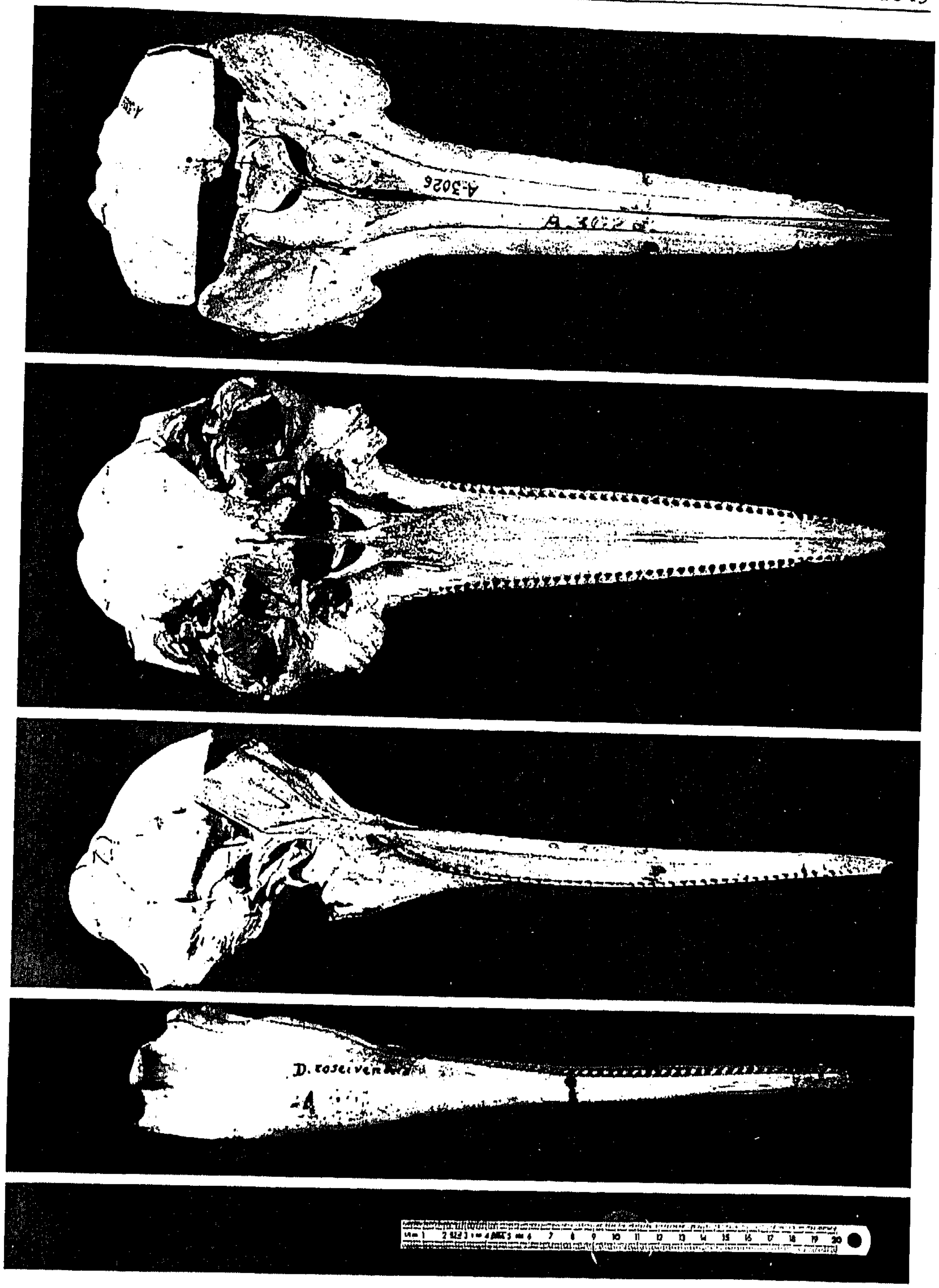

Figure 8. Dorsal, ventral and lateral photographs of the neotype specimen of *Stenella longirostris roseiventris,* MNHN A-3026.

neotype specimen can be designated (a specimen collected from the same or nearby locality as the holotype and considered to be of the same species by the first scientist who worked on the species, in this case Jacquinot). MNHN A-3026 satisfies these requirements and is therefore here designated the neo-

Table 4. Means, standard deviations (for sample sizes ≥5), sample sizes (in parentheses), and minimum and maximum values for selected cranial measurements (for cranially adult specimens; mx and pmx fused distally) and body length and postcranial measurements (for physically mature specimens; all vertebral epiphyses fused to centra) in mm (except body length in cm) for series of *Stenella longirostris longirostris* from western Pacific and Central/South Pacific and of *Stenella longirostris roseiventris* from inner Southeast Asia. Males and females listed separately for cranial characters exhibiting sexual dimorphism in eastern Pacific (Douglas *et al.* 1986) and for postcranial measurements. Skull measurements not overlapping between the series for two subspecies indicated with *. See Appendix 1 for list of specimens included.

	S. l. longirostris		*S. l. roseiventris* (Inner Southeast Asia)
	Western Pacific	Central/ South Pacific	
Condylobasal length	408.0 ± 14.63 (62) 383–468	435.8 ± 13.76 (22) 412–463	354.1 ± 11.89 (27) 335–375
Length of rostrum	262.1 ± 11.7 (62) 241–302	281.5 ± 12.88 (22) 256–304	226.8 ± 10.26 (28) 211–249
Width of rostrum at:			
base	75.3 ± 4.25 (62) 66–83	78.7 ± 3.28 (23) 73–85	62.4 ± 3.34 (30) 56–69
¼ length:			
Males	51.5 ± 3.40 (22) 45–61	54.9 ± 2.37 (9) 52–60	43.1 ± 2.02 (22) 40–47
Females	50.6 ± 3.09 (18) 45–59	54.0 ± 2.00 (9) 50–56	43.4 ± 2.88 (5) 41–48
½ length:			
Males	42.8 ± 3.23 (22) 35–51	47.2 ± 2.59 (9) 43–51	34.6 ± 1.86 (21) 31–38
Females	42.8 ± 3.61 (18) 35–49	46.3 ± 1.80 (9) 42–48	35.0 ± 1.87 (5) 33–38
¾ length:			
Males	30.4 ± 2.83 (20) 24–35	32.7 ± 1.41 (9) 31–35	24.4 ± 1.99 (22) 20–28
Females	29.1 ± 3.84 (16) 22–36	31.6 ± 1.33 (9) 29–33	24.0 ± 2.55 (5) 21–28
Width of PMXs at ½ length:			
Males	20.0 ± 1.70 (22) 17–23	20.4 ± 1.67 (9) 17–23	16.4 ± 0.98 (21) 15–18
Females	20.2 ± 2.33 (18) 17–26	21.4 ± 1.24 (9) 20–23	17.8 ± 0.84 (5) 17–19
Tip of rostrum to external nares	300.0 ± 12.53 (63) 279–346	322.7 ± 14.33 (22) 299–349	258.5 ± 11.71 (28) 242–289
Tip of rostrum to internal nares	304.8 ± 14.30 (58) 281–358	326.3 ± 14.22 (20) 299–352	258.7 ± 10.81 (25) 242–289
Preorbital width:			
*Males	143.2 ± 5.51 (22) 132–160	148.9 ± 5.25 (9) 139–156	118.5 ± 4.49 (22) 111–127
*Females	141.3 ± 6.36 (18) 128–156	150.2 ± 5.43 142–156	120.6 ± 2.61 (5) 119–125

Table 4. Continued.

	S. l. longirostris		*S. l. roseiventris* (Inner Southeast Asia)
	Western Pacific	Central/ South Pacific	
Postorbital width	157.2 ± 5.62 (63) 142–175	163.8 ± 5.27 (24) 151–172	134.4 ± 4.38 (27) 124–143
Zygomatic width:			
*Males	155.8 ± 6.03 (22) 144–173	163.1 ± 4.76 (9) 154–169	130.9 ± 4.40 (21) 121–138
Females	153.4 ± 5.98 (18) 141–166	161.9 ± 4.98 (10) 155–170	133.8 ± 4.09 (5) 131–141
Width of external nares	40.0 ± 2.13 (63) 34–45	41.4 ± 2.37 (24) 37–47	34.7 ± 2.20 (30) 29–38
Maximum width of premaxillae	61.8 ± 3.20 (62) 55–70	65.5 ± 3.16 (22) 60–70	52.5 ± 2.49 (28) 47–58
Parietal width:			
*Males	129.4 ± 4.80 (22) 119–139	132.6 ± 4.36 (9) 125–138	110.8 ± 4.28 (22) 103–117
*Females	125.9 ± 4.83 (18) 117–139	129.9 ± 4.01 (10) 124–136	108.8 ± 5.72 (5) 102–116
Height of braincase:			
Males	89.0 ± 3.00 (22) 84–95	91.3 ± 2.92 (9) 87–96	79.8 ± 3.07 (22) 76–89
Females	87.9 ± 4.70 (17) 80–96	89.7 ± 3.50 (9) 82–94	77.4 ± 2.61 (5) 76–82
Internal length of braincase:			
Males	103.2 ± 5.08 (22) 90–115	106.3 ± 3.71 (9) 99–111	93.2 ± 4.28 (22) 81–99
Females	101.6 ± 4.68 (18) 92–113	105.2 ± 1.56 (9) 103–108	94.4 ± 5.08 (5) 91–103
Length of temporal fossa:			
Males	50.1 ± 3.29 (22) 42–57	55.5 ± 3.34 (8) 50–61	48.9 ± 3.12 (22) 42–56
Females	51.3 ± 3.34 (18) 45–57	51.4 ± 4.50 (10) 47–59	48.8 ± 3.03 (5) 45–53
Height of temporal fossa:			
Males	41.5 ± 3.14 (22) 37–46	45.4 ± 4.33 (9) 39–53	42.3 ± 3.83 (22) 36–51
Females	40.8 ± 2.68 (18) 37–47	42.5 ± 3.54 (10) 37–46	41.6 ± 2.30 (5) 40–45
Length of orbit	41.2 ± 2.70 (62) 37–55	42.7 ± 1.92 (24) 39–47	38.3 ± 1.62 (28) 36–43
Length of antorbital process:			
Males	42.5 ± 3.35 (22) 32–51	44.9 ± 2.57 (9) 40–48	31.1 ± 1.92 (21) 28–35
*Females	40.5 ± 3.37 (18) 34–46	44.3 ± 2.50 (10) 40–49	30.6 ± 1.95 (5) 28–32

Table 4. Continued.

	S. l. longirostris		*S. l. roseiventris* (Inner Southeast Asia)
	Western Pacific	Central/ South Pacific	
Width of internal nares	43.7 ± 2.67 (61) 37–50	43.6 ± 43.6 (24) 39–48	34.6 ± 1.77 (26) 30–39
Length of upper toothrow	229.3 ± 12.04 (63) 209–271	245.1 ± 10.88 (22) 223–262	199.5 ± 9.61 (28) 183–222
Length of lower toothrow	225.7 ± 11.02 (61) 203–258	237.6 ± 9.24 (22) 219–253	195.7 ± 8.12 (26) 182–219
Length of ramus	352.0 ± 14.68 (59) 325–397	372.5 ± 13.96 (22) 350–398	304.3 ± 12.21 (27) 286–334
Height of ramus:			
Males	55.0 ± 2.65 (22) 51–60	58.1 ± 2.67 (9) 53–63	48.8 ± 1.88 (22) 45–52
*Females	56.4 ± 2.83 (18) 52–63	57.7 ± 1.94 (9) 54–60	49.8 ± 1.30 (5) 48–51
Width of tooth (at mid-length of lower row, transverse at alveolus)	2.34 ± 0.59 (5) 1.7–3.1	2.68 ± 0.26 (21) 2.2–3.1	2.68 ± 0.46 (6) 1.8–3.1
Body length (phy. mature):			
Males	186.7 ± 4.23 (6) 181–191	172 (1)	142.8 ± 7.70 (8) 135–158
Females	181.8 ± 10.78 (6) 167–195	—	145 (1)
Width of atlas:			
Males	74.5 ± 2.43 (6) 71–77	78 (1)	62.9 ± 2.75 (8) 59–66
Females	72.5 ± 3.62 (6) 67–78	—	64 (1)
Height of atlas:			
Males	46.7 ± 2.66 (6) 42–50	48 (1)	38.6 ± 1.74 (9) 36–40
Females	46.5 ± 3.02 (6) 42–51	—	37 (1)
Width of first thoracic:			
Males	84.2 ± 7.73 (5) 74–92	42 (1)	59.0 ± 3.42 (7) 54–64
Females	73.8 ± 7.98 (5) 64–83	—	57 (1)
Width of first lumbar:			
Males	44.0 ± 1.67 (6) 41–46	43 (1)	32.9 ± 2.03 (9) 30–36
Females	42.0 ± 3.41 (6) 38–46	—	35 (1)

Table 4. Continued.

	S. l. longirostris		*S. l. roseiventris* (Inner Southeast Asia)
	Western Pacific	Central/ South Pacific	
Length of longest rib:			
Males	258.2 ± 8.47 (6) 247–272	248 (1)	196.3 ± 9.30 (8) 180–208
Females	255.5 ± 17.07 (6) 231–275	—	204 (1)
Height of scapula:			
Males	115.5 ± 3.27 (6) 111–120	113 (1)	89.6 ± 7.02 (9) 75–97
Females	111.8 ± 5.78 (6) 103–120	—	94 (1)
Length of scapula:			
Males	114.2 ± 8.47 (6) 101–123	106 (1)	91.3 ± 8.49 (9) 77–102
Females	109.3 ± 12.60 (6) 92–131	—	89 (1)
Length of humerus:			
Males	53.7 ± 1.51 (6) 52–55	—	44.5 ± 1.52 (6) 42–46
Females	48.6 ± 5.55 (5) 41–55	—	45 (1)
Length of radius:			
Males	73.5 ± 3.39 (6) 68–77	71 (1)	62.3 ± 3.64 (7) 57–67
Females	71.8 ± 2.95 (5) 69–75	—	65 (1)
Length of ulna:			
Males	63.3 ± 2.58 (6) 59–66	—	52.5 ± 2.43 (6) 49–55
Females	60.8 ± 3.19 (5) 57–65	—	58 (1)
Length of longest chevron bone:			
Males	45.0 ± 3.52 (6) 41–51	45 (1)	29.9 ± 2.67 (7) 26–33
Females	44.5 ± 2.43 (6) 41–47	—	33 (1)
Length of pelvic bone:			
Males	74.8 ± 7.19 (6) 63–82	—	67.3 ± 6.11 (3) 59–74
Females	62.6 ± 9.34 (5) 51–75	—	57 (1)
Width of widest vertebra:			
Males	175.3 ± 7.39 (6) 163–182	188 (1)	129.8 ± 6.11 (6) 122–138
Females	177.2 ± 13.83 (5) 159–192	—	140 (1)

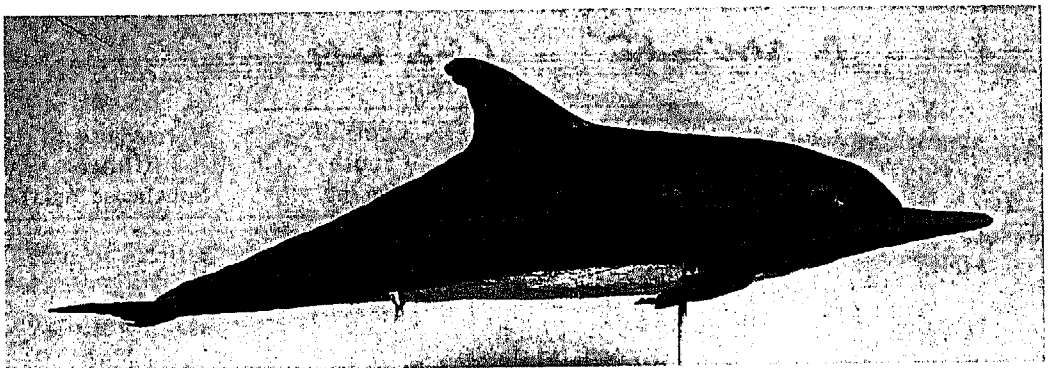

Figure 9. Mounted whole specimen MNHN-GCZ no. 19, paraneotype of *Stenella longirostris roseiventris.*

type specimen for *Delphinus roseiventris* (now *Stenella longirostris roseiventris*), and the other two skulls and the mounted specimen from the expedition in the Paris Museum as paraneotypes.[5] At this time, the two postcranial skeletons cannot be assigned to the skulls with confidence.

Redescription of the Subspecies

Stenella longirostris roseiventris (Wagner, 1846)

Neotype—MNHN A-3026, skull only, Arafura Sea ("*mer des Moluques*"), illustrated in Figure 8.

[5] This situation is in accord with the letter but unfortunately not the spirit of the ICZN. A strictly legalistic solution has yielded a neotype which by all rights should be a lectotype. Perhaps a future emendment of the Code may bring it more in line with the historical realities of taxonomic research.

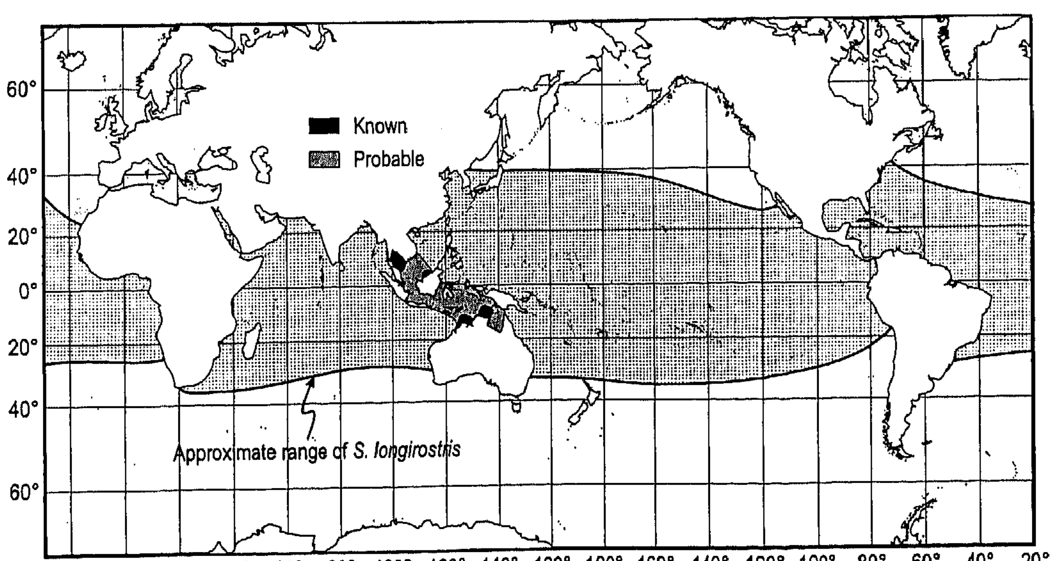

Figure 10. Known and probable geographic range of *S. l. roseiventris.* Range of *S. longirostris* modified from Jefferson *et al.* (1993).

Referred specimens—Gulf of Thailand: NSMT M24851, 24971, 24973–24975, 24979, 24852. Arafura Sea: MNHN A-3027 (paraneotype), 1928-192 (paraneotype), 1880-553 (postcranial only), 1880-554 (postcranial only), MNHN-GCZ no. 19 (mounted whole; paraneotype; illustrated in Fig. 9); NTM 510, 520, 525, 656, 657, 696-699, WAM m-26630, 28129, 28132–28134, 28139, 28141, 28142, 28144–28150. Timor Sea: NTM u-284, 514, 516, 522, 536. Western Australia: WAM m-26622, 26623, 26628. Sarawak, Malaysia: FMNH 99608.

Diagnosis—A subspecies of *Stenella longirostris* characterized by distinct tripartite color pattern (Perrin *et al.* 1989, fig. 3), erect to falcate dorsal fin, relatively small postanal hump, relatively small adult body size (to about 158 cm; average about 145 cm; Table 2), proportionately large flippers and dorsal fin, relatively short (335–375 mm) and narrow (zygomatic width 121–141 mm) adult skull (Table 3), relatively low number of teeth (41–52 per row; Table 4) and relatively low number of vertebrae (28–32; Table 4).

Distribution—Shallow inner waters of Southeast Asia, including the Gulf of Thailand, Timor and Arafura Seas, and similar waters of Indonesia, Malaysia and northern Australia (Fig. 10). Replaced in deeper and outer waters by larger pelagic subspecies *S. l. longirostris* (Gray, 1828).

Description of neotype—Measurements (in mm) of the neotype skull (* = from True, 1889): condylobasal length 375*, length of rostrum 244*, width of rostrum at base 69, width of rostrum at ½ length 37, width of rostrum at ¾ length 26, greatest preorbital width 119, zygomatic width 137, parietal width 112, height of left temporal fossa 43, length of left upper toothrow 216, length of left ramus 327. Teeth: lower left 48*. External size, shape and coloration unknown. Other skulls illustrated in Van Beneden and Gervais 1880, Perrin *et al.* 1989; those in former do not correspond in detail to MNHN specimens and may be composite drawings.

Variation—Number of vertebrae may be lower off northern Australia than in the Gulf of Thailand (Fig. 4). Skull size may vary within the range; the two largest known skulls are from the easternmost part of the range covered by collections (neotype and paraneotype).

Specimens examined—All of the referred specimens were examined.

Geographical Variation Within the Large Pelagic Form

It has been previously noted (Perrin 1990) that adult body size and skull size may vary geographically in *S. l. longirostris.* The results here indicate that such variation does exist. Average adult skull length is greater in the Central and South Pacific than in the western Pacific and Philippines (Fig. 2, 7). Average adult body size may also be greater (Fig. 1), but the data for specimens known to be physically mature are too few to allow a firm conclusion.

Three adult or near-adult specimens from Cairns, Queensland (QM jm-4716, 4718, and 4719) associate closely with other western Pacific specimens in toothcounts and cranial proportions (Fig. 6) but are at or near the lower end of the distributions of body length and skull size, close to the upper end of the distributions for the small form, *S. l. roseiventris.* This suggests that spinner dolphins inhabiting the Great Barrier Reef region, albeit of the large pelagic form, may be smaller than those in deeper-water areas to the north and east; larger samples will be necessary to further address this question.

The Philippine series contains a single very large skull some 34 mm beyond the upper end of the range for the other specimens, at 468 mm the largest skull examined in the study (Fig. 2). In a similar situation in the eastern tropical Pacific, a "whitebelly" spinner dolphin from a zone of hybridization or intergradation between *S. l. longirostris* and *S. l. orientalis* to the east was over 30 cm larger than the next-largest spinner dolphin known from the region and yielded a skull of 468 mm, the same size as the large Philippine specimen (Perrin *et al.* 1985, Perrin 1990). These are the two largest skulls known for the species globally. In the Pacific, spinner dolphins with skulls approaching this size occur in the Central and South Pacific (Fig. 7). There are at least two possible explanations for the two anomalously large skulls in the eastern and western Pacific: they may have been cases of endocrinally induced gigantism, or they may represent immigration from the Central or South Pacific.

Genetics results to date are consistent with little or no genetic interchange between the two subspecies (comparison of mtDNA RFLP haplotypes between northern Australian (*S. l. roseiventris*) and eastern Pacific (*S. l. longirostris*/*S. l. orientalis*) series showed no overlap (Dizon *et al.* 1991), nor did a similar analysis of mtDNA control-region sequence haplotypes (García-Rodriguez 1995), but further analyses including Philippine large-form spinners are needed to determine the extent of gene flow between the two forms in Southeast Asia.

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Appendix 1

Specimens Examined

Stenella longirostris roseiventris—See *Referred specimens* in redescription of subspecies.

Stenella longirostris longirostris—Hawaii: BMNH 1965.8.25.1; CAS 10529, 16455–16458; LACM 27093, 27095, 54049, 54050, 54056, 54057, 54060, 72296; MCZ 51700; MMBL 1194, NSMT M24615, 24815; SWFSC 0028, 0030–0034; USNM 339649, 504140, 504470. Kure Atoll, U.S.: USNM 243860. Midway Island, U.S.: BBM 157118. Rangiroa Atoll (Tuamotus, France): USNM 504252. Hiva Oa (Marquesas, France): USNM 504253. Teraina (Line Islands, Kiribati; formerly Washington Island): USNM 504251. "Christmas Island" (Teraina?): ANSP 3065, 3066. Phoenix Islands, Kiribati: NSMT M26633. Nagasaki Pref., Japan: NSMT MS5100, 24800. West of Kyusyu, Japan: NSMT M2700. Arno Atoll, Marshall Islands: USNM 291958. Solomon Islands: NSMT M24928, 24931, 24933, 24934; BMNH 1966.11.18.7. Nauru: NSMT M24929. Bismarck Archipelago: NSMT M24930, 25373. Near Caroline Islands: NMST M24932, 25376. Ifaluk Atoll, Caroline Islands: USNM 297851, 297852. Enewetok Atoll, Marshall Islands: USNM 395404. Madang, Papua New Guinea: AM M27951. New South Wales, Australia: AM M21266. Cairns, Australia: QM JM4716, 4718. Philippines: SUML 2, 4, 9–12, 14–16, 39–45, 48, 49, 65–67, 73–100, 103, 110, 119, 120, 123–125, 127, 128, 713–724, 727, 732–734. Lamalera, Indonesia (eastern Indian Ocean): WAM M18643. Browse Island, Australia (eastern Indian Ocean): WAM M39970. Sumatra (eastern Indian Ocean): USNM 49661. Unknown localities: RMNH 8676 (holotype of *S. longirostris* (Gray, 1828)), BMNH 349a (holotype of *Delphinus microps* Gray, 1846), BMNH 1471a/1850.6.5.7 (holotype of *Delphinus stenorhynchus* Gray, 1866), BMNH 847a/1847.7.6.2 (holotype of *Delphinus alope* Gray, 1846).

Appendix 2

Museum and Collection Acronyms

AM, Australian Museum, Sydney; BBM, Bishop Museum, Honolulu; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts; MMBL, Marine Mammal Biological Laboratory (now National Marine Mammal Laboratory), Seattle; MNHN, Muséum national d'Histoire naturelle, Paris; NSMT, National Science Museum, Tokyo; NTM, Northern Territories Museum, Darwin; QM, Queensland Museum, Brisbane; RMNH, Rijksmuseum, Leiden; SUML, Silliman University Marine Laboratory, Dumaguete, Philippines; SWFSC, Southwest Fisheries Science Center (Marine Mammal Synoptic Collection), La Jolla, California; WAM, Western Australian Museum, Perth.