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INTRODUCTION

We reviewed the subspecies listed by Rice (1998) and those described since (a total of 49, in 19 species), assessing them against the criteria recommended by the recent Workshop on Shortcomings of Cetacean Taxonomy in Relation to Needs of Conservation and Management (Reeves et al., 2004). The workshop suggested that the subspecies concept can be construed to cover two types of entities: a) lineages diverging but not quite far along the continuum of divergence (still having significant gene flow with another lineage or lineages) to be judged as species, and b) lineages that may well be species but for which not enough evidence is yet available to justify their designation as such. As a criterion for support of a subspecies, the workshop suggested as a guideline that there be at least one good line of either morphological or appropriate genetic evidence. "Appropriate" was not defined; the recommendation was that that be left up to the taxonomist authors of subspecies and to their professional peers. A further recommendation was that evidence on distribution, behavior and ecology should be considered not as primary but as supporting evidence, as there was not agreement at the workshop that such characters are necessarily stable (in the case of distribution) or inherent (behavior and ecology).

RESULTS

Common minke whale, *Balaenoptera acutorostrata* Lacépède, 1804

1. *Balaenoptera acutorostrata scammoni* Deméré, 1986 [North Pacific]

The subspecies had its origin in *Balaenoptera davidsoni* Scammon, 1872 described from the eastern North Pacific. Deméré (1986) noted that the name *B. davidsoni* was preoccupied by *B. davidsonii* Cope, 1872, a fossil whale described a few months earlier. He gave the taxon a new name, *B. acutorostrata scammoni*, designating it as a subspecies in recognition of the fact that Tomilin (1957) and Hershkovitz (1966) had synonymized *B. davidsoni* with *B. acutorostrata* but that Tomilin (1957) and others had recognized the subspecific status of North Pacific minke whales.

Scammon (1872) did not describe any morphological features that are not concordant with Lacépède's original description of *B. acutorostrata* from the North Atlantic, noting pointed head, size (27 feet – Lacépède said 8—9 meters), protrusion of lower jaw, narrower upper jaw, white baleen (longest about 10 inches; 170 plates on one side – Lacépède said about 200), flippers and flukes light below, and white band on the flippers. Scammon noted that his species was "nearly allied to the *B. rostrata* [= *B. acutorostrata*] as far as description will admit of instituting a comparison."

True (1904) pointed out some minor differences in bone relationships between the very small series of skulls available from the North Atlantic and North Pacific (2 of each) and noted that they might be significant if constant. Cowan (1939) compared external and cranial measurements for skulls of 2 adults from the Atlantic and 3 from the North Pacific and found small differences in body proportions, number of baleen plates, and cranial and postcranial characters. He concluded that "Should the..differences be substantiated there would be grounds for recognizing *Balaenoptera davidsoni* as a subspecies of *B. acutorostrata* Lacépède but in the light of present knowledge taxonomic recognition of a Pacific species is apparently not justified." Tomilin compared slightly larger series (7 for North Atlantic and 3 for the western North Pacific) and concluded that the former had a relatively longer rostrum (67.2% of skull length vs. 62.6%) and considered the difference "significant" [1967 translation]. However, given the small sample sizes the results cannot be considered meaningful, and Tomilin himself considered the subspecies "weakly expressed." Similar conclusions were reached by Omura and Sakiura (1956) and Omura (1957) based on specimens from Japan. Thus there appears to be no strong morphological basis for the subspecies; the differences detected are not significant considering the small sample sizes.

A neighbor-joining analysis of mtDNA control region sequences (300bp) yielded a North Pacific clade separated from North Atlantic whales by four fixed differences (Baker et al. 2000). Another analysis of mtDNA control region sequences (340bp) yielded a strongly supported clade (bootstrap 100%) in a neighbor-joining tree, sister to a clade composed of whales from the North Atlantic and Brazil in the southern hemisphere (Pastene et al., 2007). The two in turn were sister to a clade of "dwarf minke whales" from the Antarctic (undescribed subspecies discussed below).

True (1904), Cowan (1939), Omura and Saikura (1956), Tomilin (1957), Omura (1957) and Hershkovitz (1966) concluded that the subspecies was weakly defined. The genetic coherence of the North Pacific samples in the analyses by Baker et al. (2000) and

Pastene et al. (2007) is a line of evidence supporting the subspecies. However, no clear quantitative criteria have been established concerning what constitutes appropriate genetic evidence for a subspecies, and in the absence of morphological evidence, recognition in this case must be tentative (indicated by asterisk in table below).

Balaenoptera acutorostrata acutorostrata Lacépède 1804

The nominate subspecies was first referred to with a trinomial name by Tomilin (1957) along with his account of *B. a. davidsoni* (now *B. a. scammoni*). If the "dwarf minke whale" of the southern hemisphere is at some point formally described as a subspecies and given a trinomial scientific name, subsequent use of the nominate subspecies (which would include all the common minke whales in the North Atlantic) would be firmly justified.

Balaenoptera acutorostrata subsp. (un-named) [Dwarf minke whale of southern hemisphere]

Rice (1998) recognized a third subspecies, "*B. a.* subsp." based on Best's (1985) description of a "diminutive form" of minke whale off Durban, South Africa that contrasted with larger and differently colored animals (subsequently recognized as Antarctic minke whales, *B. bonaerensis*). Arnold et al. in 1986 described two forms of minke whale from Australian waters, dubbing the smaller "dwarf minke whale" and concluding that they were of the same form as the small whales from South Africa. Pastene et al. (2007) reported the range of *B. acutorostrata* (as the un-named subspecies) as extending to Antarctic waters during the austral summer. Minke whales identified as the same form have also been reported from Brazil (Zerbini et al., 1996).

Most morphological comparisons in the literature are with the larger Antarctic minke whale (now *B. bonaerenis*), hence the "dwarf" appellation, but some differences from northern-hemisphere common minke whales are evident and relatively consistent. The most striking difference is in coloration. Rather than bearing a simple white band, the flipper is distally black and proximally white, with the white portion connecting to a roughly oval white patch embedded in a large light blaze on the shoulder. There is a light blaze on the thorax. The white baleen bears a dark-brown fringe that is absent in the northern hemisphere. Albeit based on small sample sizes, the dwarf form has a proportionately broader skull (Perrin and Brownell, 2009) and may differ in other skull features. Arnold et al. (2005) concluded, "There appears to be sufficient grounds to recognize the two southern forms (the dwarf form and the form eventually recognized as the species *B. bonaerensis*) as taxonomic entities, at least as subspecies."

Antarctic dwarf minke whales comprised a strongly supported clade (bootstrap 100%) in a maximum-likelihood tree based on mtDNA control region sequences (340bp) (Pastene et al., 2007). However, the relationships may be more complicated. In an alternative genealogical analysis of the same sequences using the quartet-puzzling method (QP) by Pastene et al., 2007), two dwarf whales from Brazil grouped with North Atlantic common minke whales (as a sub-clade with two of them) and one with the Antarctic dwarf whales (QP reliability values 84 and 76, respectively).

While more work is needed on larger series of osteological specimens, the external morphological and genetic results provide adequate justification for formal description of the dwarf minke whale as a subspecies of *Balaenoptera acutorostrata.*

However, before any new name is proposed for this subspecies it will be necessary to determine the taxonomic status of nominal species described from the region that are presently junior synonyms of *B. acutorostrata* or *B. bonaerensis*, such as *Balaenoptera huttoni* Gray, 1871, described from Otago Head Bay, New Zealand.

Sei whale, *Balaenoptera borealis* Lesson, 1828

Balaenoptera borealis schlegelii (Flower, 1865) [Southern hemisphere]
        Flower compared a skull and skeleton from Pekalongan, Java with those of sei whales from Europe including Lesson's holotype and concluded, "…all we can say, after having compared them bone by bone and found them agreeing in every particular, is that there is no proof of their being of different species, and that therefore, in the absence of other evidence, we are obliged to consider them identical." However, because of a reluctance to include in the same species forms occurring at such great distance from each other (in northern Europe and Southeast Asia), he went with the practice of the times and created the new species *Sibbaldius* [= *Balaenoptera*] *schlegelii* based on the Java specimen. The holotype is in the Leiden Museum of Natural History and was received from the northwest coast of Java in 1864, which is a tropical location and well outside the normal range of sei whales. However, based on the illustration in Van Beneden and Gervais (1868--1879) and photographs (provided to RLB by T. Yamada) the specimen appears to be a sei whale.
        Tomilin (1946) synonymized *B. borealis* and *S. schlegelii* but retained the subspecies *B. borealis borealis* for the northern hemisphere and *B. borealis schlegelii* for all sei whales from the southern hemisphere, including those in the tropics (e.g. Java) and the Antarctic. This was based on whaling data showing that average size was greater in the Antarctic than in the North Atlantic. He posited that lower water temperatures in the Antarctic led to greater body size (for all of the balaenopterids).
        It is not known whether all sei whales in the southern hemisphere migrate to the Antarctic, including those from low latitudes (e.g. latitude of Java, the type locality for *B. b. schlegelii*) and therefore are all larger than those in the northern hemisphere as per Tomilin's data and hypothesis. If some sei whales are resident at lower latitudes, they too may be smaller. And it is even possible that the Java whale was a vagrant from the northern hemisphere. Thus the morphological justification for the subspecies is weak.
        A maximum-parsimony phylogeny of baleen whales aimed at identifying regional sources of sei-whale market products (Baker et al. 2004) exhibited a strongly supported clade of North Atlantic samples (bootstrap support 96%) but a weakly supported (<50%) clade containing both southern hemisphere and North Pacific samples. One New Zealand sample was sister to a three-way polytomy of one Hawaii sample, seven Hawaii samples and the rest of the southern hemisphere samples, with low bootstrap support (<50%) for both nodes. Genetic support for the southern-hemisphere subspecies at present is weak.

Balaenoptera borealis borealis Lesson, 1828 [Northern hemisphere]
        Validity of this subspecies (nominate trinomial first used by Tomilin, 1946) depends on substantiation of subspecies-level distinctness of *B. b. schlegelii* as applied to all sei whales in the southern hemisphere. However, no series of specimens have been

compared either morphologically (other than in total length in whaling statistics) or genetically between the northern and southern hemispheres. In fact, very few specimens exist from the southern hemisphere.

Fin whale, *Balaenoptera physalus* (Linnaeus, 1758)

Balaenoptera physalus quoyi Fischer, 1829 [Southern hemisphere]
This subspecies first appeared as *Balaena rostrata australis* described by Desmoulins in 1822. He used the trinomial but referred to the form as a species. The name *Balaena rostrata australis* was preoccupied by *Balaena australis*, which Desmoulins had applied to the southern right whale earlier in the same paper. Fischer (1829) therefore renamed the taxon *Balaenoptera quoyi*, interpreting Desmoulins' form with a trinomial name as being a species. Desmoulins noted that his holotype whale (not collected), observed by Quoy in the Falkland Islands/Malvinas, was twice as long as whales of the species *B. rostrata* (minke whales) in the North Atlantic. His descriptions of baleen, dorsal fin and throat grooves match the fin whale. Lönnberg (1931) recognized this and placed the form in the synonymy of the fin whale, as *B. physalus quoyii* (later corrected to *B. p. quoyi* by Tomilin (1957)). Lönnberg interpreted the name to apply to all fin whales in the southern hemisphere.
No morphological justification for the split has been offered other than the larger average size of fin whales in the Antarctic as opposed to those in the northern hemisphere, supposedly engendered by the cold Antarctic water (Tomilin, 1946). The same problem obtains here as for the sei whale. The holotype of *B. physalus quoyi* is from the Falkland Islands/Malvinas. If some fin whales are resident in lower latitudes of the southern hemisphere (not usually migrating to the Antarctic), and if one accepts Tomilin's hypothesis that larger size is connected to cold water, the lower-latitude whales may not be larger than their northern relatives. Indeed, Clarke (2004) noted smaller size of fin whales from lower latitudes in his paper proposing a new subspecies *B. p. patachonica* based on *B. patachonica* Burmeister 1865. Antarctic fin whales may be distinctive in size, but they may comprise a subspecies apart from the taxon based on the Falklands/Malvinas specimen.

Balaenoptera physalus physalus (Linnaeus, 1758) [Northern hemisphere]
Validity of the nominate subspecies (again, trinomial first used by Tomilin, 1946) depends on substantiation of subspecies-level distinctness of *B. p. quoyi* as applied to all fin whales in the southern hemisphere.

Blue whale, *Balaenoptera musculus* (Linnaeus, 1758)

Balaenoptera musculus indica Blyth, 1859 [Northern Indian Ocean]
As noted by Rice (1998), before the evaluation of Linnaeus' sources by True in 1899, *Balaenoptera musculus* was applied to the fin whale; blue whales were usually known as *B. sibbaldi* (Gray, 1847). However, Blyth described his whale of the northern Indian Ocean as a species, *B. indica*, with no inference of connection with the fin whale.

The holotype from Burma [Myanmar] was reported as 84 feet long; another of the same type of 90 feet was reported. The holotype was in error reported missing by Branch and Mikhalev (2008) but one of us (RLB) examined the specimen in the Calcutta Museum, and it is a blue whale. Hershkovitz (1966) placed *B. indica* in the synonymy of *B. musculus*. Most modern cetologists accept the assignment to the blue whale mainly because there are no modern confirmed records of the fin whale from the northern Indian Ocean, while there are many recent records of blue whales. Tomilin (1946) did not include the subspecies in his list of rorquals, although he included *B. m. musculus* and *B. m. intermedia* (discussed below); first use of the trinomial *B. musculus indica* was by Brownell and Donaghue (1994), followed by Rice (1998).

The genetic comparison (mtDNA and microsatellites) of southern-hemisphere "true" and pygmy blue whales by LeDuc et al. (2007) included two samples from the Maldives, but they did not fall out as different from other Indian Ocean whales from farther south off South Africa and Australia. However, LeDuc et al (2007) only examined 420 base pairs.

Branch and Mikhalev (2008) reexamined illegal Soviet catch data for blue whales from regions in the northern and southern Indian Ocean. Blues whales from the northern Indian Ocean were 0.5 -0.6 m shorter than pygmy blue whales (*B. m. brevicauda*) taken in the western (Madagascar) and eastern Indian Ocean (Australia). These differences were statistically significant, but these authors believed that the smaller total length of the NIO blue whales did not support them being recognized as a separate subspecies. Mikhalev (2000) also showed that the reproductive season of NIO blue whales, based on the illegal Soviet specimens, was offset by six months when compared to Antarctic blue whales. We believe that the available data (smaller total length and reproductive isolation) do support the recognition of the NIO blue whales as a separate subspecies.

An additional line of evidence that strongly supports the isolated status of the northern Indian Ocean blue whales is their unique acoustic call (Alling *et al*. 1991). Blue whales are well known for the production of high intensity, low frequency, long duration acoustic calls which have been documented to be constant in character over decadal time scales (McDonald *et al* 2006).

Balaenoptera musculus intermedia Burmeister, [1871-72] [Southern hemisphere high latitudes, in summer]

Burmeister (1871--72) described *B. intermedia* from the nearly complete skeleton and baleen of a whale found floating near the mouth of the Río Luján near Buenos Aires. Its large size and black baleen identify it as a blue whale. Tomilin (1946) recognized *B. musculus intermedia* as representing the blue whales of the southern hemisphere, hypothesizing as for the other balaenopterids that the cold water of the Antarctic led to greater size than in the northern hemisphere. Validity of this scheme is problematic because of the apparent existence of two morphological forms of blue whales in the southern hemisphere: "true" blue and pygmy blue whales (discussed below). It is not known to which of these morphotypes the Argentine specimen belonged (the locality is within the range of both), therefore the proper application of the names *B. m. intermedia* and *B. m. brevicauda* may other than presently used; the latter may be a synonym of the former. This question could only be resolved with development of a reliable "ancient-DNA" genetic method for classifying specimens to the two forms and application of the

method to a sample taken from the type specimen in the Buenos Aires Museum (if that specimen still exists).

Balaenoptera musculus brevicauda Ichihara, 1966 [Southern mid-to-high latitudes, in summer]

Ichihara (1961) first pointed out the existence of two blue whale morphotypes in the southern hemisphere. Whales taken in 1959/60 from around Kerguelen Island (49 degrees S), which he called "pygmy blue whales," differed on average from whales captured in Antarctic waters to the south ("true blue whales"); the Kerguelen whales were shorter (females maturing on average at 68 feet, or 10 feet shorter), had proportionately shorter baleen plates, a more "silvery" vs. steel-gray coloration, and possibly different body proportions (a shorter length of the body posterior to the anus). He presented the results (including confirmation of the difference in body proportions) at the First International Symposium on Cetacean Research in Washington, D.C. in 1963 (Norris, 1966), dubbing the pygmy blue whale *B. m. brevicauda.* The holotype, a complete skeleton, was deposited in the Marine Science Museum, Tokai University, Shimizu, Japan (Yamada pers. comm. 25 IX 2009 to RLB), and a single baleen plate (M9287) was deposited at the National Science Museum, Tokyo (Ichihara 1966). Before the paper appeared in print (Ichihara, 1966), Zemsky and Boronin (1964) presented additional data confirming Ichihara's results and suggesting that the pygmy form was more similar to blue whales of the northern hemisphere than to Antarctic blue whales. They used the trinomial before the subspecies was formally published, but the name in this case appeared as a *nomen nudum*, and Ichihara's 1966 description retains priority.

Branch *et al*. (2007) re-examined all available commercial catch data for blue whales in the Southern Hemisphere and showed that mean total lengths of sexually mature females from Antarctic waters were 83.4 – 86.3 ft (25.6 – 26.6 m) while pygmy blue whale adult females were only 68.9 ft, 21.0 m long. They also showed that the mean total length of adult blue whales taken off Chile was intermediate between these at 77.1 ft (23.5 m) and suggested that these whales may comprise an additional subspecies.

LeDuc et al. (2007) examined genetic relationships (in mtDNA sequences of 420bp of the control region and in allelic frequencies of 7 microsatellites) between putative pygmy and "true blue" whales. The task was hampered by the difficulty of reliably identifying the two forms at sea (the two forms overlap on the feeding grounds). Some whales field-identified as "true blue whales" and biopsied prove to be genetically more closely related to others field-identified as pygmy blue whales, and vice versa. Despite this difficulty, higher- (Antarctic) and lower-latitude samples were highly differentiated. However, the difference was not greater than that between low-latitude whales from the Pacific Ocean (Chile) and Indian Ocean, suggesting that additional taxonomic subdivision may eventually be appropriate. The genetic relationships among blue whale populations globally are presently under investigation.

The morphological data comprise a strong line of evidence for recognition of the subspecies. However, the use of the name *B. m. brevicauda* for the pygmy form is clouded by the problem of the unknown identity of the type specimen of *B. m. intermedia* from Argentina and uncertain relationship with blue whales in the northern hemisphere (all known at this point as *B. m. musculus*). In addition, if *B. m. indica* and *B. m.*

brevicauda were shown to be the same, *B. m. brevicauda* would become a junior synonym.

Balaenoptera musculus musculus (Linnaeus, 1758) [Northern hemisphere]
       Tomilin (1946) first used this trinomial, suggesting that it apply to all blue whales of the northern hemisphere, which he thought smaller than all blue whales of the southern hemisphere (his *B. m. intermedia*). The more recent data showing variation at smaller geographic scales suggest that it may not be that simple. In any case, given the number of potential forms, it is likely that the name will survive, perhaps applying only to blue whales of the North Atlantic.

South Asian river dolphin, *Platanista gangetica* (Lebeck, 1801)

Platanista gangetica minor (Owen, 1853) [Indus River drainage]
       This subspecies was first described as the species *Platanista indi* authored by Blyth in 1859. Blyth described his specimen from the Indus River as being larger and more robust and with stouter teeth than the dolphins from the Ganges. Anderson (1878) found no difference between the two forms and placed *P. indi* in the synonymy of *P. gangetica*. However, Pilleri and Gihr (1971) found differences in the maxillary crest of skulls from the Ganges and Indus and revived the two-species scenario. Kasuya (1972) noted that the differences found by Pilleri and Gihr (1971) were average differences not separating the two series and re-affirmed existence of a single species. He recommended subspecies status for the two forms: *P. g. gangetica* and *P. g. minor*. He also found average differences in external proportions between them, the Indus dolphin having a longer peduncle (distance from anus to fluke notch). Van Bree (1976) pointed out that *P. indi* is a junior synonym of *P. minor* Owen, 1853. Owen described the Indus dolphin as a variety of smaller size with smaller teeth, ironically the opposite of Blyth's later assertion.
       The average morphological differences described by Pilleri and Gihr (1971) and Kasuya (1972) well justify subspecies status for the two forms. The ranges are disjunct, although the Ganges and Indus systems may have been connected in the geological past (Pilleri et al., 1982).

Platanista gangetica gangetica (Lebeck, 1801) [Ganges River drainage]
       The nominate subspecies is a morphologically well-supported taxon restricted to the Ganges River drainage.

Amazon river dolphin, *Inia geoffrensis* (Blainville in Desmarest, 1817)

Inia geoffrensis boliviensis D'Orbigny 1834 [Amazon drainage above rapids in Bolivia]
Inia geoffrensis geoffrensis (Blainville in Desmarest, 1817) [Amazon drainage below rapids]
       These two subspecies will likely be elevated to species.
       D'Orbigny described *Inia boliviensis* as an "espéce unique" in his new genus *Inia*. He did not contrast or compare it with Blainville's earlier (1817) *Delphinus geoffrensis*.

Hershkovitz (1966) placed *I. boliviensis* in the synonymy of *I. geoffrensis*. Van Bree and Robineau (1973) compared the holotypes of the two species and found only a greater number of teeth (>30/row) in the skull from Bolivia. They agreed with Hershkovitz' joining of the species but recommended recognition of two subspecies: *I. g. geoffrensis* and *I. g. boliviensis.* Pilleri and Gihr (1977) documented a number of average osteological differences between the two forms based on series of specimens and recommended that they be again elevated to species status. They noted likely complete isolation of the Bolivian animals by 400 km of severe rapids. They further described a subspecies of their *I. geoffrensis* (discussed below). They presented a dichotomous key for identification of specimens to the two species and the subspecies, based on relationships of the bones of the skull, relative length of the rostrum and number of teeth. Casinos and Ocaña (1979) dismissed the osteological variation as probably clinal and recommended acceptance of one species, with no subspecies. They opined that the perhaps complete isolation of the Bolivian animals by river rapids was likely of too-recent origin to merit taxonomic attention. Best and da Silva (1989) supported recognition of a single species, on the grounds that too few specimens had been studied and too little evidence produced for allopatric speciation. More recent classifications (e.g., Rice, 1998; Perrin et al., 2009) have considered the dolphins to consist of one species with three subspecies, although additional morphological studies have suggested the existence of two species (da Silva, 2009).

Recent genetic studies have provided strong evidence of complete isolation and substantial divergence of the Bolivian form, based on mtDNA control region sequences (Banguera-Hinestroza et al., 2002) and nuclear Y-chromosome and autosomic intron sequences (Ruiz-Garcia et al., 2008), that support recognition of the two species, and it is likely that the split will be reflected in future cetacean classification lists and databases.

Inia geoffrensis humboldtiana (Pilleri and Gihr, 1977) [Orinoco River drainage]
Pilleri and Gihr described this subspecies to include dolphins in the Orinoco River drainage, based on a relatively shorter rostrum than in the Amazon system. The morphological evidence is weak because of small sample size. Genetic evidence for a split between Orinoco and Amazon dolphins is weak for mtDNA control-region sequences (Banguera-Hinestroza et al., 2002) but strong based on fixed differences in sequences of nuclear introns (Ruiz-Garcia et al., 2008). However, the geographical coverage of the samples across the Amazon/Orinoco border region is poor (with roughly 2,000 km of river separating the closest samples of the two putative forms).

Short-beaked common dolphin *Delphinus delphis* Linnaeus, 1758
Long-beaked common dolphin *Delphinus capensis* Gray, 1828

The long-beaked common dolphin was relatively recently elevated from the synonymy of *Delphinus delphis* (Hershkovitz, 1966; Rice, 1977) to a full species (Rice, 1998; Perrin et al., 2009), based on color pattern and cranial morphology (Heyning and Perrin, 1994) and a study of mtDNA control-region and cytochrome-*b* sequences (Rosel et al., 1995). However, more recent studies of patterns in mtDNA sequences (Natoli et al., 2006; Amaral et al., 2009) have uncovered non-concordance of morphological and

genetic data in global populations of common dolphins. The validity of the current species-level taxonomy is in doubt, and rigorous revision is badly needed. However, the currently recognized subspecies are considered here on their individual merits alone, apart from the question of what species they may finally reside in. The nominate subspecies are not covered, as their fates rest on the revision of the genus.

Delphinus delphis ponticus Barabash, 1935 [Black Sea]

Barabash described the subspecies based on external measurements of >20,000 dolphins taken in the Black Sea commercial dolphin fishery. The dolphins were on the average smaller (by about 20--30cm) than common dolphins in the adjacent Mediterranean and Atlantic, later confirmed by comparison with larger samples from those bodies of water (Reilly and Perrin, 1984; Perrin, 1985). Kleinenberg (1956) examined a series of skulls and disputed the subspecies status. However, metrical and non-metrical multivariate discriminant analyses of cranial characters correctly identified 97.8% and 83.6%, respectively, in a jackknife analysis of a mixed sample of 181 skulls from the Black Sea, Western North Atlantic and Eastern North Pacific (Perrin et al., 1994). The geographical series differed from each other significantly in a number of individual measurements.

Rosel et al. (1995) found Black Sea samples dispersed among short-beaked samples from other regions in a phylogenetic tree based on her mtDNA analysis. Similar results were obtained by Natoli et al. (2008) in a minimum spanning network based on both 428 bps of the mtDNA control region and in analysis of nine microsatellites.

The two lines of morphological evidence (body size and cranial configuration) justify recognition of this subspecies.

Delphinus capensis tropicalis van Bree, 1971 [northern Indian Ocean to Southeast Asia]

The subspecies was first described by G. Cuvier (1829) as *Delphinus longirostris*, based on the skull of a long-beaked dolphin collected by Dussumier in Malabar, Bay of Bengal, India. The skull had 55—60 teeth in each row. He stated that the scientific name was bestowed by Dussumier [in an unpublished manuscript]. Blanford (1888--91) noted that the name *Delphinus longirostris* was preoccupied by *D. longirostris* Gray, 1828 (now *Stenella longirostris*) and gave the form the new name *Delphinus dussumieri*. However, that name was also preoccupied, by *Delphinus dussumieri* Fischer, 1829, proposed as a name for *Delphinus capensis* G. Cuvier, 1829, preoccupied by *D. capensis* Gray, 1828, and van Bree (1971) re-christened the form *Delphinus tropicalis*. Rice (1998) treated it as a full species.

Jefferson and Van Waerebeek (2002) measured 86 skulls from the supposed range of the species (Middle East to China) and found the form to have an exceptionally long rostrum and high tooth counts, different from other "long-beaked" dolphins from the western Pacific, southwestern Indian Ocean and eastern North Pacific. They proposed that it be considered a subspecies (of the putative long-beaked species *Delphinus capensis*). However, they also noted a clinal situation, with the dolphins having slightly shorter rostra to the east, south and west, approaching those of long-beaked dolphins beyond the range of the form in those regions. Thus the data do not suggest existence of a single coherent geographic form, but rather a series of populations grading from long-

beaked in the southern Indian Ocean, Mid East and Southeast Asia to extremely long-beaked around the Indian subcontinent.

Samples from 24 dolphins identified as *D. capensis tropicalis* did not occupy an unique position in a cytochrome *b* median-joining network based on 279 animals from around the world but were mixed with long-beaked dolphins from the North Pacific and various short-beaked dolphins (Amaral et al., 2009).

The subspecies is not strongly supported by either the morphological or the genetic evidence.

Delphinus capensis capensis Gray, 1828 [eastern Atlantic, southeastern Indian Ocean and eastern and western Pacific]

Gray described the species *Delphinus capensis* based on a stuffed skin (with skull inside) from the Cape of Good Hope, South Africa. The skull was later removed. Heyning and Perrin (1994) reported that measurements of the skull associated it with the long-beaked form from California (previously assigned to *Delphinus bairdii* Dall, 1873 (Banks and Brownell, 1969), and applied Gray's name as the oldest available. As noted above, this taxonomy is not in accord with molecular data. The validity of the subspecies rests on recognition of *D. capensis tropicalis*.

Common bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821)

Tursiops truncatus ponticus Barabash-Nikiforov, 1940

Barabash-Nikiforov (1940, 1960) compared Black Sea specimens to published data from distant populations and concluded that a Black Sea subspecies exists. The features he noted in his 1940 paper for the Black Sea specimens had on average smaller body, smaller skull, abbreviated rostrum relatively broad at base, fewer teeth, and expansion of the premaxillaries of the skull at midlength of the rostrum weakly expressed or absent (Tomilin, 1957). Kleinenberg (1956) disagreed with the concept of a Black Sea subspecies, suggesting that the sample sizes compared were too small. Barabash-Nikiforov later (1960) noted differences in external dimensions and coloration. Viaud-Martinez et al. (2008) examined a large series of skulls from the Black Sea and the adjacent Mediterranean and confirmed some of Barabash-Nikiforov's findings; they concluded that the Black Sea specimens were significantly different from those in the Mediterranean in several measurements and were able to discriminate among Black Sea, Mediterranean and Atlantic specimens with 100% accuracy.

Based on analysis of 442 base pairs of the mtDNA control region, Viaud-Martinez et al. (2008) concluded that the Black Sea common dolphins differ genetically from those in the Mediterranean and Atlantic, due to geographic isolation. Thus the subspecies is strongly supported by both morphological and genetic evidence.

Tursiops truncatus truncatus (Montagu, 1821)

The nominate subspecies as presently recognized applies to common bottlenose dolphins globally apart from those in the Black Sea. The subspecies is not a coherent evolutionary lineage; as noted above, for example, specimens from the Mediterranean are distinguishable both morphologically and genetically from those in the adjacent Atlantic.

Further, morphologically and genetically different coastal and offshore forms have been described from several regions (Hoelzel et al., 1998; Natoli et al., 2004), and a distinct form off southern Australia has been suggested to represent a separate species (Möller et al., 2008).

Pantropical spotted dolphin, *Stenella attenuata* (Gray, 1846)

Stenella attenuata graffmani (Lönnberg, 1934) [Coast of eastern tropical Pacific]
      Lönnberg described the species *Prodelphinus* [= *Stenella*] *graffmani* based on a single dolphin from near Acapulco, noting that it was collected "by a bullet through the head." The specimen he examined consisted of only a salted skin with the jaws and the terminal vertebrae retained inside. He decided it was a new species based on color pattern, size, external proportions and size and proportions of teeth. Perrin (1972, 1975) examined an osteological series of large spotted dolphins collected by harpoon on the coast of southern Mexico-Central America in comparison with spotted dolphins collected from bycatch in the tuna purse-fishery farther off shore and concluded that both were assignable to *Stenella attenuata* (Gray, 1846), which had been previously applied (as *Prodelphinus attenuatus*) to dolphins of the same form from the Indian Ocean (True, 1894) and Hawaii waters (True, 1903), a conclusion supported by a later revision of the spotted dolphins (Perrin et al., 1987). The two eastern Pacific series overlapped morphologically, but the large coastal form differed in average size, degree of spotting, and cranial characters (also see Perrin et al., 1987 for comparison of 31 coastal with 575 offshore specimens). Perrin therefore retained the taxon as the subspecies *S. attenuata graffmani.* The cranial morphological distinction was confirmed by Douglas et al. (1984).
      An analysis of mtDNA and microsatellites (Escorza-Treviño and Dizon, 2000) yielded significant separation between most coastal populations and the adjacent offshore animals.
      The lines of morphological and genetic evidence support recognition of the subspecies.

Stenella attenuata attenuata (Gray, 1846)
      The nominate subspecies includes all pantropical dolphins around the globe except the coastal form in the eastern tropical Pacific (Perrin, 2001). Perrin described "subspecies A" based on offshore animals in the eastern Pacific and "subspecies B" based on Hawaiian specimens, but the latter was based on a small sample not strongly distinguishable from the eastern Pacific series and the former on the series from only a portion of the range of the form extending across the tropical Pacific. These nominal un-named subspecies have not been generally recognized (Perrin, 2001; Perrin et al., 2009).
      As more samples are collected from other parts of the world, additional subspecies are likely to be recognized.

Spinner dolphin, *Stenella longirostris* (Gray, 1828)

Stenella longirostris orientalis Perrin, 1990 [Offshore eastern tropical Pacific]

Perrin (1972, 1975) described the "eastern spinner" based on a large series of dolphins collected from bycatch in the tuna purse-seine fishery in the eastern tropical Pacific and authored the subspecies in 1990. It differs from spinner dolphins from elsewhere in the world's tropical waters in size, external form (a distinctive forward-canted dorsal fin in the adult male, correlated with large post-anal hump and upturned fluke tips) and coloration. The skull differed modally from those of spinner dolphins in the coastal waters of Central America and the adjacent central Pacific (confirmed from larger samples by Douglas et al., 1991). While the eastern spinner in its external morphology and coloration is strikingly distinct from other spinner dolphins, specimens from the western fringes of the range of the form ("whitebelly spinners") grade into the morphology of animals to the west in the central Pacific, suggesting subspecific rather than specific status.

The morphological line of evidence supports the subspecies.

Stenella longirostris centroamericana Perrin, 1990 [Coast of Central America]

Perrin (1972, 1975) described this subspecies as the "Costa Rican spinner" and later (1990) gave it a trinomial name and re-dubbed it "Central American spinner." It possesses the coloration (with smaller ventral light patches) and distinctive adult-male dorsal fin of *S. l. orientalis* but is larger and has a proportionately longer rostrum. Differences between the series in body size and skull characters were sharp, but the sample size for the Central American form in the original analysis was small. However, an aerial survey demonstrated average size of adult female Central American spinners at 198cm vs. 172cm for eastern spinners, based on sample sizes of 20 and 956, respectively (P<0.01 in Tukey –Kramer test; Perryman and Westlake, 1998).

The morphological evidence supports recognition of the subspecies.

Stenella longirostris roseiventris (Wagner, 1846) [Inner Southeast Asia]

Wagner based *Delphinus roseiventris* on the small *dauphin à ventre rose* described by Jacquinot from Indonesian waters in a series of expedition reports (1842—1853). Perrin et al. (1999) re-described the subspecies, applied Wagner's name and designated a neotype specimen. The neotype skull falls within the range of a form in inner Southeast Asian waters sharply differentiated from other spinner dolphins in body size, external proportions, number of teeth, number of vertebrae, cranial characters, habitat and ecology. The morphological evidence supports this subspecies.

Stenella longirostris longirostris (Gray, 1828)

The nominate subspecies applies to spinner dolphins westward from the Central Pacific, through the Indian Ocean, to the tropical Atlantic, excluding those in central Southeast Asia. Limited data from regions within that span (e.g., Robineau and Rose (1983) and Van Waerebeek et al. (1999) for the western Indian Ocean and Cadenat and Doutre (1959) for the eastern Atlantic) suggest the likely existence of more forms deserving of subspecies status. Perrin (1972, 1975) described two un-named subspecies from the eastern and Central Pacific, "subsp. C [whitebelly spinner]" and "subsp. D [Hawaiian spinner]," but the former likely represents a zone of hybridization or intergradation between eastern spinners and those to the west (Perrin et al., 1985; Perrin et al., 1991), and the latter represents only a small portion of the range in the central and

western Pacific (Perrin, 1998). Rice (1998) did not list these two nominal un-named subspecies.

A difficulty with this nominate subspecies is that the holotype specimen is from an unknown locality. It is likely polytypic, but full resolution of the taxon into its component (subspecific) parts may be difficult or impossible unless the holotype skull is unequivocally assignable to a particular region through morphological or molecular means.

Dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828)

Lagenorhynchus obscurus fitzroyi (Waterhouse, 1838) [Southern South America]

Waterhouse described *Delphinus fitzroyi* based on a drawing and the tail and jaws of a dolphin from the coast of Patagonia. He contrasted it based in coloration with *Delphinus superciliosis* Lesson and Garnot (1826), which Gray (1846) later synonymized with *L. obscurus*, described from the Cape of Good Hope.

Rice (1998) interpreted the subspecies to include dusky dolphins from both coasts of South America. Dusky dolphins in Peru and Chile differ significantly from both those in South Africa and New Zealand in skull morphology (Van Waerebeek, 1993, with 96.5, 91.7 and 90.9% of individuals, respectively, successfully identified in a discriminant analysis). Greatest difference, in skull size, an average 8.5%, was between Peru/Chile and both South Africa and New Zealand. However, a median-joining network based in the full mtDNA genome (Cassens et al., 2003) indicated three fixed differences between dusky dolphins from Peru and Argentina, more differentiation than between either and specimens from South Africa (New Zealand was not included in the analysis), suggesting that the subspecies should be considered to contain dusky dolphins from the southwest Atlantic, excluding those from the west coast of South America.

Lagenorhynchus obscurus obscurus (Gray, 1828) [southern Africa]

Rice (1998) included in the nominal subspecies dusky dolphins from the west coast of southern Africa and Île Amsterdam, based on the morphological results of Van Waerebeek (1993). However, given the uncertain subspecific status of dusky dolphins from Peru/Chile based on the molecular results, the nominal subspecies may need to be more inclusive, containing dolphins from more than one distribution. In principle the available data would seem to support existence of at least 4 subspecies.

Lagenorhynchus obscurus subsp. (un-named) [New Zealand dusky dolphin]

As noted above, dusky dolphins from New Zealand are separable in cranial characters from those in Peru/Chile and South Africa (Van Waerebeek, 1993). The main differences from South African animals are smaller tooth size and a greater number of teeth (P<0.0001 and 0.001, respectively in *t* tests). Rice (1998) recognized "*L. o.* subspecies" for dolphins from New Zealand, the Auckland Islands, Campbell Island and the Chatham Islands. The morphological differentiation supports recognition of the subspecies.

Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804)

Cephalorhynchus commersonii kerguelenensis (Robineau, Goodall, Pichler and C. S. Baker, 2007) [Kerguelen Islands]

This recently described subspecies is supported by differences in body length, coloration, cranial measurements and tooth counts (n = 12 for Kerguelen and 67 for South America); all except tooth counts were absolute differences. There was one fixed difference between five mtDNA haplotypes from Kerguelen (n = 11) and eight from South America (n = 35), suggesting possible movement between the two populations of one individual per generation. Additional supporting evidence is provided by disjunct distribution and differing acoustic behavior. The authors noted that the morphological and genetic evidence reaches the level of the guideline for subspecies recommended by the 2004 workshop (Reeves et al., 2004).

Cephalorhynchus commersonii commersonii (Lacépède, 1804) [Southern South America]

Lacépède described *Delphinus commersonii* from the Straits of Magellan, Tierra del Fuego, Chile. Given the well-supported Kerguelen subspecies and the limited range of the remaining populations of the species (cold temperate waters of southern South America and the Falkland Islands/Malvinas), the nominate subspecies in this case is likely a coherent (non-divisible) subspecies. It is well-supported by several lines of evidence as summarized above.

Hector's dolphin, *Cephalorhynchus hectori* (Van Beneden, 1881)

Hector (1872, 1872[1873]) described *Electra clancula* from New Zealand based on Gray's (1846) *Lagenorhynchus clanculus* from an unknown locality. His figures clearly depict a Hector's dolphin. Van Beneden described another specimen from New Zealand and noted its resemblance to Hector's specimen and that *E. clancula* [misspelled *clangula* in his paper] was preoccupied by Gray's (1868) *Electra clancula* from Chile. He renamed the species *Electra hectori*. Hector (1885) placed the species in Gray's (1846) genus *Cephalorhynchus.*

Cephalorhynchus hectori maui A. Baker, Smith and Pichler, 2002 [North Island of NZ]

More than 75% (84%) of skulls from North Island (n = 13) and South Island (n = 46), New Zealand were separable based on rostrum width at half-length (Baker et al., 2002); a discriminant function based on this measure and rostrum length successfully identified 100% of the specimens. The two populations also differ in average body length and coloration. The subspecies is supported by strong morphological evidence. Molecular evidence concordant with existence of two subspecies includes unique mtDNA haplotypes and near fixation of rare or unique microsatellite alleles (Pichler et al., 1998).

Cephalorhynchus hectori hectori (Van Beneden, 1881) [South Island of NZ]

The nominate subspecies is limited to South Island, New Zealand and is well-differentiated from *C. h. maui* on the North Island coast (discussed above). As such, it is a well-supported coherent subspecies that is not likely to be subdivided.

Long-finned pilot whale, *Globicephala melas* (Traill, 1809)

Globicephala melas edwardii (A. Smith, 1834[1835]) [Cold-temperate southern hemisphere]

Smith based *Phocaena edwardii* on a description and drawing given to him by an E. Verreaux of a whale stranded near the Cape of Good Hope; he did not mention collection of a specimen. The whale had a rounded head with a small pointed beak, large pointed dorsal fin located at mid-body length, and 12 teeth in each jaw. The description does not well match that of a pilot whale, which has a rounded dorsal fin located nearer the head than the tail. True (1889) noted the contradictory details of the description but placed the species in the synonymy of *Globicephalus* [= *Globicephala*] *melas*, with an implication that the species had a continuous distribution from the North Atlantic to the Cape.

The skull examined by Fraser (1950) as the putative holotype specimen of *Phocaena edwardii* (BM53.9.18.26) and listed as such by Hershkovitz (1966) is not the holotype. Fraser identified the BM specimen as *Globicephalus macrorhynchus* based on lateral expansion of the premaxillaries. Furthermore, he counted 9 teeth in each jaw, as opposed to the 12 reported by Smith. Peter van Bree located a skull of *G. melas* in the Bordeaux Museum (van Bree et al. 1978) with the data, "Cap de Bonne Espérance, VIII-1831, rapporté par Jules Verreaux" that he believed to be the holotype of *Phocaena edwardii*. He noted that Jules Verreaux and his brother Eduard (the "E. Verreaux" referred to by Smith in his description) collected material in South Africa for the Paris Museum and other museums in France. In the same paper, he concluded that in consideration of the minor differences from the northern form, the long-finned pilot whales of the southern hemisphere should be considered a subspecies of *G. melas*, with junior synonyms *G. chilensis* (Philippi, 1896) and *G. leucosagmaphora* (Rayner, 1939), to which Fraser assigned specimens from the Falklands and New Zealand.

Recognition of the subspecies is based primarily on the disjunct antitropical distribution of the species. The only morphological character described by Rayner (1939) as different for the southern form was a more pronounced (white) saddle mark. However, van Bree concluded that southern pilot whales with even a faint (gray) saddle mark, like that in northern long-finned pilot whales, were *G. melas*. Davies (1960) found the mark to be absent in some individuals in a school of southern long-finned pilot whales and concluded that the mark is variable in both northern and southern populations. He did recommend retention of two subspecies, but based only on the antitropical distribution. Thus there is no strong line of morphological evidence supporting the subspecies. However, the separation of the northern and southern whales by a vast region of tropical and temperate waters suggests that this is a case where reconsideration of distribution as a primary criterion might be justified.

Globicephala melas melas [Northern hemisphere]

The nominate subspecies includes long-finned pilot whales of the North Atlantic and the extinct population identified by Kasuya (1975) in the North Pacific. Its recognition rests on recognition of *G. melas edwardii.* The very small number of skulls available for the North Pacific do not allow meaningful comparison with whales in the North Atlantic.

Killer whale, *Orcinus orca* (Linnaeus, 1758)
    Orcinus orca subsp. (un-named) [WNP Transients]
    Orcinus orca subsp. (un-named) [WNP Residents]
    There are presently no recognized named subspecies of the killer whale. However, in a status review of Southern Resident killer whales, a U.S. Government scientific panel concluded that the Southern Resident whales comprise a distinct population segment (DPS) of an un-named Resident subspecies distinct from an un-named Transient subspecies (Krahn et al., 2004). The two subspecies were held to differ on average in morphology (dorsal-fin size and shape, saddle-patch shape, pigmentation and skull characters), to be divergent in both mtDNA and nuclear markers, and to differ in ecology and behavior, including acoustic dialects and practices. The existence of two subspecies was acknowledged in subsequent protection of the Southern Resident DPS under the U.S. Endangered Species Act.
    The genetic, ecological and behavioral differences between Transient and Resident killer whales are well established (Ford, 2009; Hoelzel et al., 2007), but data supporting the morphological differentiation have not yet appeared in the published literature. The genetic line of evidence (e.g., fixed differences in mtDNA sequences) can be considered strong.
    Orcinus orca orca (Linnaeus, 1758) [Global apart from Residents and Transients]
    The nominate subspecies will not come into existence formally unless/until the putative Resident and Transient subspecies are described and receive trinomial names.

Finless porpoise, *Neophocaena phocaenoides* (G. Cuvier, 1829)

Neophocaena phocaenoides asiaeorientalis (Pilleri and Gihr, 1972) [Yangtze River]
Neophocaena phocaenoides sunameri (Pilleri and Gihr, 1975) [Temperate w. Pacific]
    The histories of these two subspecies are complex and intertwined. Pilleri and Gihr described the species *Neomeris* [= *Neophocaena*] *asiaeorientalis* from the Yangtze and adjacent coast of the East China Sea based on statistically significant average differences in cranial and postcranial characters from finless porpoises of the Indian Ocean. Van Bree (1973) noted that Pilleri and Gihr's name was actually a synonym of the preoccupied name *Delphinus melas* Schlegel, 1841-1843, based on specimens from Japan, providing analyses showing no statistically significant differences between the series from China and from Japan described by Mizue et al. (1965). He also noted that the generic name *Neomeris* is preoccupied by a worm and that the next name in priority is *Neophocaena*, as previously recognized by Hershkovitz (1961, 1966). Of most relevance to this review, he expressed the belief that average differences do not constitute sufficient grounds for recognition of separate species and demoted the Chinese/Japanese form to

the subspecies *N. phocaenoides asiaeorientalis.* Pilleri and Gihr (1975) rejected this argument and moreover presented analyses showing differences between the Chinese series and an expanded series from Japan justifying (in their minds) description of a yet a third species, *Neophocaena sunameri* Pilleri and Gihr, 1975 for finless porpoises in Japanese and Korean waters. Rice (1977) questioned whether the Japanese and Chinese populations were sufficiently separable to warrant recognition of *N. sunameri* even as a subspecies. Gao (1991 thesis and 1995 paper with Zhou) employed RFLP analysis and re-examined morphology (including the dorsal tubercle patch) and concluded existence of three subspecies, with *N. p. asiaeorientalis* restricted to the Yangtze population. Amano et al. (1992), however, concluded based on further morphological analyses that subspecific status was justified for the Chinese/Japanese populations combined, as *N. p. asiaeorientalis,* and the finless porpoises in the Indian Ocean/Southeast Asia as the nominate subspecies. P. Wang (1992) compared animals from three regions in Chinese waters and found differences in the extent and configuration of the dorsal tubercle patch. He concluded that three forms were present, which he referred to *N. p. phocaenoides* (in the South China Sea, presumably contiguous with those in the Indian Ocean), *N. p. asiaeorientalis* (in the East China Sea and Yangtze River) and *N. p. sunameri* (in the Bohai Sea and Yellow Sea). Rice (1998) recognized the three subspecies but like Gao (1991) relegated porpoises from the East China Sea coast to *N. p. sunameri* along with Korean and Japanese animals rather than to *N. p. asiaeorientalis* as was done by P. Wang (1992). Yang et al. (2002) found differentiation in mtDNA sequences (720 bp of control region) among the three geographical regions (excluding Japan) as defined by Rice (1998); differences were greater between either the Yangtze or Yellow Sea series and the South China Sea series than between the two more northern series. They did not apply subspecific names to the series. Jefferson (2002) examined specimens from throughout the range of the species and concluded based on cranial morphology that there exist two forms: the "*asiaeorientalis*-type" in coastal and riverine waters of Japan, Korea and northern China (with two geographic populations, in the Yangtze River and in other more northern East Asian waters) and the "*phocaenoides*-type" from the South China Sea through the Indian Ocean to the Persian Gulf (with three geographic populations). He suggested that complete separation of the two forms in width of the dorsal tubercle ridge might indicate existence of two species. However, Jefferson and Hung in their 2004 Mammalian Species account recognized three subspecies, with *N. p. asiaeorientalis* restricted to the Yangtze River. In their distribution map they depicted an overlap of the ranges of *N. p. sunameri* and *N. p. phocaenoides* in the region of the Taiwan Strait, unusual in cetacean taxonomy in the recognition of partially sympatric subspecies. Most recently, J. Wang et al. (2008) concluded that reproductive isolation is present between the two forms in the area of sympatry based on the difference in tubercle ridge (consistent with genetic data) supported the suggestion by Jefferson (2002) that the two types may represent separate species.

The strong morphological and molecular evidence support recognition of the two subspecies *N. p. asiaeorientalis* and *N. p. sunameri* as defined by Gao (1971) and Jefferson and Hung (2004), with the caveat that together they may constitute a species separate from *N. phocaenoides.*

Neophocaena phocaenoides phocaenoides (G. Cuvier, 1829) [Tropical Indian and W. Pacific]

G. Cuvier (1829) described *Delphinus phocaenoides* very briefly, "M. Dussumier à[sic] découverte au Cap, une espèce de ce sous-genre, qui a la tête ronde, et les dents comprimées et obtuses du marsouin (*D. phocaenoides*,)(3)."

The description is obviously of a finless porpoise and the skull was identified as such by later workers, but the type locality is in question. Allen (1923) believed that a stuffed skin of a right whale dolphin, *Lissodelphis peronii*, from the Cape of Good Hope was somehow erroneously associated by Cuvier with Dussumier's finless porpoise skull. In researching Dussumier's journals, he found no mention of collection of specimens at the Cape and concluded that the finless porpoise skull was collected elsewhere. He also noted that the finless porpoise had not since been recorded from South Africa. Hershkovitz (1966) rejected Allen's arguments and noted that Gibson-Hill (1950) reported occurrence of the species off South Africa. However, the South African record was based on a sighting, identified only on the basis of absence of a dorsal fin, a feature also of the southern right whale dolphin, which has been subsequently recorded from as far north on the coast of southern Africa as Namibia (Rose and Payne, 1991). Dussumier did report collecting (for the Paris Museum) on the Malabar coast of India a species similar to the beluga in having a blunt head and no dorsal fin (Laissus, 1973), certainly a finless porpoise, and the type locality of the nominate subspecies is now accepted to be the Malabar coast (Jefferson and Hung, 2004).

The morphological and molecular differences between this form and the two described from East Asia (discussed above) provide strong grounds for recognizing the subspecies.

Harbor porpoise, *Phocoena phocoena* (Linnaeus, 1758)

Phocoena phocoena vomerina Gill, 1865 [North Pacific]

Gill described the species *Phocaena* [= *Phocoena*] *vomerina* based on a skull from Puget Sound and a skull and skin from San Francisco. He compared it with *Phocaena communis* [= *Phocoena phocoena*] as having a vomerine bone "more developed and recurved backwards, expanding below into a more or less enlarged horizontal process behind the palatines" and more numerous teeth (39-40 in each upper jaw). Tomilin (1957) demoted the species to a subspecies and characterized the form as more differentiated from the Azov-Black Sea form (*P. p. relicta*, discussed below) than from the North Atlantic form (*P. p. phocoena*) by "higher development of the condylar width and the occipital condyles, and, possibly, greater size of the skull." He also stated that it was unknown whether this form differed from the North Atlantic form in dentition (the difference claimed by Gill – 1865). Amano and Miyazaki (1992) demonstrated pronounced differences between North Pacific and North Atlantic series of skulls based on multivariate analysis of 15 cranial measurements. The Pacific specimens on average had relatively longer rostrums and tooth rows, narrower skulls, and more teeth.

Rosel et al. (1995) sequenced the mtDNA control region of harbor porpoises from the North Pacific (n= 81), North Atlantic (15) and Black Sea (9) and found no shared

haplotypes and high genetic divergence among the series, e.g. 5.1% between North Pacific and North Atlantic.

The strong lines of morphological and molecular evidence support recognition of the subspecies.

Phocoena phocoena relicta Abel, 1905 [Black and Azov Seas]

Abel (1905) in a mostly paleontological paper based the species *Phocaena* [= *Phocoena*] *relicta* on a skull and 2 photographs given to him by the director of the Russian Academy of Sciences research station at Sebastopol on the Black Sea. He found differences from *Phocaena communis* [= *P. phocoena*] in a number of cranial bones and their relationships and in the shape of dental roots. However, his account suffers from the typical paleontologist's practice of arguing from single specimens. Tsalkin (1940) offered no further morphological comparisons but considered the form a subspecies. Tomilin (1957) agreed; he noted that the Black Sea form differs from porpoises from the North Atlantic and North Pacific in having average lesser height of the occipital condyles and narrower condylar width, as well as absence of tubercles on the front margins of the dorsal fin and flippers, citing studies of series of specimens by Barabash-Nikiforov (1940). Viaud-Martínez et al. (2007) compared 45 specimens from the Black Sea with 132 from the North Atlantic and concluded that the Black Sea form on average is smaller, has a smaller skull, wider and long rostrum, lesser orbital length, smaller internal nares, lesser condylar width, and larger occipital ridge than porpoises from the North Atlantic.

Viaud-Martínez et al. (2007) also sequenced the first 364 base pairs of the mtDNA control region for 93 porpoises from the Black Sea and 49 from the Sea of Marmora, Aegean Sea and North Atlantic and found no shared haplotypes and strong differentiation between the Black Sea and the North Atlantic, suggesting separation for thousands of years. They concluded that the Black Sea form is on a separate evolutionary pathway and should be recognized as a subspecies.

The subspecies is strongly supported by the morphological and molecular results.

Phocoena phocoena phocoena (Linnaeus, 1758) [North Atlantic]

Linnaeus described the species *Phocoena phocoena* based on earlier descriptions of porpoises in the "Oceano Europaeo Baltico." As noted above, Amano and Miyazaki (1992) demonstrated strong morphological differentiation between harbor porpoises of the North Pacific and North Atlantic, and Rosel et al. (1995) found pronounced parallel genetic differentiation. However, the nominate subspecies must still be considered as possibly containing more than one form, as there is an apparently isolated population of larger-bodied porpoises with larger skulls on the Atlantic coast of northern Africa that has not been fully assessed against North Atlantic porpoises (Fraser, 1958; Smeenk, 1992).

Phocoena phocoena subsp. (un-named) [Western Pacific harbor porpoise]

Rice (1998) listed "*P. p.* subsp." from the western Pacific based on Amano and Miyazaki's (1992) finding that skulls from Japan and the U.S. west coast were "distinctly different." However, those authors did not recommend recognition of a separate subspecies in the western Pacific, stating that distribution of the species was continuous

across the North Pacific. Rice noted a distributional gap in the Aleutian Islands between Shemya and Unimak. Given the lack of morphological data for specimens from the large parts of the nearly continuous range between Japan and the U.S. west coast, the justification for recognition of a western Pacific subspecies apart from the eastern form is weak. Genetic relationships between eastern and western North Pacific porpoises have not been examined.

Dall's porpoise, *Phocoenoides dalli* (True, 1885)

Phocoenoides dalli truei Andrews 1911
Phocoenoides dalli dalli (True, 1885)
   These subspecies are unusual in that they are based on two morphotypes that were originally thought to occur on opposite sides of the North Pacific but are actually more complexly distributed and partially sympatric (at least seasonally) in the western Pacific.
   Andrews (1911) described the species *Phocoenoides truei* based on a single carcass from Japan. He noted close cranial similarity to *Phocoenoides dalli* but described a number of external differences: forward extension of the lateral white area, a patch of gray on the lower surface of the peduncle, a differing coloration in the anal region, deeper shape of the peduncle, and flukes black on both sides vs. having white markings. However, Benson and Groody (1942) reported a specimen from California that was intermediate in coloration between the patterns described for the two species, noted that the two forms were alike in external form, skull and postcranial skeleton (demonstrated by comparison of Andrew's description with the photograph in Miller (1930), and placed *P. truei* in the synonymy of *P. dalli.* Tomilin (1957) followed this lead but retained the subspecies *P. dalli truei*, noting the difference in extent of the lateral white area. Thus the only morphological character separately the two putative subspecies was (and is) a color-pattern difference, with a not-uncommon intermediate pattern described.
   In the report of a survey in the northwestern Pacific, Kasuya and Jones (1984) noted that the "*truei*-type" was limited to Japanese coastal waters, with the number sighted east of 155° "negligible" and that the *"dalli*-type" reached sexual maturity as a smaller size. Miyazaki et al. (1984) reported mixed feeding areas for the two forms. Based on sighting cruises in Japanese waters and adjacent regions, Miyashita and Kasuya (1988) reported that "*dalli*-type" individuals occurred throughout the range of the species in the western Pacific, wintering for the most part in the Sea of Japan and summering in the Okhotsk Sea and on the Pacific coast of Japan. *"Truei*-type" porpoises were seen only off the Pacific coast of northern Japan and southern Kuril Islands. Despite this confused picture of geographically intermingled types, Jefferson (1988) accorded subspecies status to the two forms, noting that their taxonomic status was not firmly settled.
   In 1992, Szczepaniak and Webber reported a "*truei*-type" porpoise from California. Rice (1998) opined that "geographical variation in the color-phase ratio is sufficient to permit the recognition of two subspecies," with *P. d. truei* consisting of <5% "Dalli-phase" and >95% "Truei-phase" and occurring in a limited area of the western North Pacific immediately east of the southern Ostrowa Kuril'skiy, Hokkaido, and the Sanriku coast of Honshu. He characterized *P. d. dalli* as >99% "Dalli-phase" and <1% "Truei-phase" and ranging in subarctic waters from the southeastern Sea of Okhotsk, the

southern Bering Sea, and the northern Gulf of Alaska, south to the Sea of Japan, the Subantarctic Boundary at about 42° across the North Pacific, and in the California Current to about 32° N off Baja California Norte, Mexico, except in the areas occupied by *P. d. truei.*

Amano et al. (2000) reported a third color-pattern morph in the *dalli*-type porpoises from the Sea of Japan, with greater distance from the tip of the beak to the forward edge of the white flank patch than in other *dalli*-type animals. Hayano et al. (2003) analyzed mtDNA control-region sequences (479bp, with flanking tRNA genes) and detected genetic differentiation among the three populations, with pairwise difference being greatest between the Sea-of-Japan *dalli*-type population and the other *dalli*-type population and *truei*-type population, which were insignificantly different from each other. Escorza-Treviño et al. (2004) analyzed 379 base pairs of the mtDNA control region and 6 microsatellites for 23 *truei*-type and 113 *dalli*-type. The mtDNA haplotypes clustered in two distinct clades, each containing both color morphs. However, at the population level, they found significant differentiation between sympatric populations of the two forms. They argued that differentiation between the two forms is at the population level, much as was found for 9 putative populations of the *dalli*-type (Escorza-Treviño and Dizon, 2000). Subsequently, Amano and Hayano (2007) found based on genetic and morphological evidence that the *dalli* and *truei* types are nearly completely isolated, with seasonal admixture accounting for the earlier findings of only population-level differentiation. They concluded that three subspecies should be recognized: the *truei*-type and the two *dalli*-types (Sea-of-Japan/Okhotsk Sea and North Pacific) with different color patterns. The balance of morphological and genetic evidence favors this scheme. However, recognition of the two separate *dalli*-form subspecies must await their formal description and assignment of trinomial names. For the present, the nominate subspecies *P. dalli dalli* stands as a catch-all for forms other than *P. dalli truei.*

CONCLUSIONS AND DISCUSSION

Of the 49 subspecies, 38 in our opinion meet the guideline criterion suggested by the 2004 workshop of support by at least one line of morphological or genetic evidence (Table 1). One subspecies, the North Pacific minke whale *Balaenoptera scammoni*, is supported only by genetic evidence. We recommend provisional recognition of this subspecies but conclude that more work is needed to clarify the issue of what constitutes "appropriate" genetic evidence in support of a subspecies. For example, the 75% rule often used in morphological delimiting of a subspecies may have a molecular analog.

We also conclude that further attention should be given to the question of whether or not a broad gap in distribution (as for long-finned pilot whales in the northern and southern hemispheres) should be considered a strong line of evidence. If it were, an additional six subspecies would perhaps be accepted (marked with two asterisks in Table 1).

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Table 1. Subspecies reviewed, with indication of support by morphological (MOR) or genetic (GEN) evidence. Subspecies supported by neither in bold. Single asterisk indicates tentative conclusion; two asterisks (under MOR) indicate case without strong morphological or genetic support but supported by distributional evidence. Three asterisks indicate nominate subspecies now known to contain two subspecific-level un-named taxa. Note that "Supported" for nominate subspecies means only that it is supported in relation to other described subspecies, without implication that it is a single coherent evolutionary lineage, unless explicitly so documented.

SUBSPECIES	SUPPORTED	
	MOR	GEN
Balaenoptera acutorostrata acutorostrata Lacepède, 1804	X	X
B. acutorostrata scammoni Deméré, 1986		X*
B. acutorostrata subsp. (un-named)[Dwarf minke whale]	X	X
***Balaenoptera borealis borealis* Lesson, 1828**	**	
***B. borealis schlegelii* (Flower, 1865)**	**	
***Balaenoptera physalus physalus* (Linnaeus, 1758)**		
***B. physalus quoyi* Fischer, 1829**		
Balaenoptera musculus musculus (Linnaeus, 1758)	X	X
B. musculus indica Blyth, 1859	X	
***B. musculus intermedia* Burmeister, [1871—1872]**		
B. musculus brevicauda Ichihara, 1966	X	X
Platanista gangetica gangetica (Roxburgh, 1801)	X	
P. gangetica minor (Owen, 1853)	X	
Inia geoffrensis geoffrensis (Blainville, 1817)	X	X
I. geoffrensis boliviensis D'Orbigny, 1834	X	X
***I. geoffrensis humboldtiana* (Pilleri and Gihr, 1977)**	**	
Delphinus delphis delphis Linnaeus, 1758	X	
D. delphis ponticus Barabash, 1935	X	
***Delphinus capensis capensis* Gray, 1828**		
***D. capensis tropicalis* van Bree, 1971**		

Tursiops truncatus truncatus (Montagu, 1821)	X	X
T. truncatus ponticus Barabash-Nikiforov, 1940	X	X
Stenella attenuata attenuata (Gray, 1846)	X	X
S. attenuata attenuata graffmani (Lönnberg, 1934)	X	X
Stenella longirostris longirostris (Gray, 1828)	X	
S. longirostris orientalis Perrin, 1990	X	
S. longirostris centroamericana Perrin, 1990	X	
S. longirostris roseiventris (Wagner, 1846)	X	
Lagenorhynchus obscurus obscurus (Gray, 1828)	X	
L. obscurus fitzroyi (Waterhouse, 1838)	X	
L. obscurus subsp.(un-named) [New Zealand dusky dolphin]	X	
Cephalorhynchus commersonii commersonii (Lacepède, 1804)	X	X
C. commersonii kerguelenensis Robineau et al., 2007	X	X
Cephalorhynchus hectori hectori (Van Beneden, 1881)	X	X
C. hectori maui A. Baker et al., 2002	X	X
***Globicephala melas melas* (Traill, 1809)**	**	
***G. melas edwardii* (A. Smith, 1834[1835])**	**	
Orcinus orca orca (Linnaeus, 1758)	X	X
O. orca subsp. (un-named) [WNP Residents]	X	X
O. orca subsp. (un-named) [WNP Transients]	X	X
Neophocaena phocaenoides phocaenoides (G. Cuvier, 1829)	X	X
N. phocaenoides asiaeorientalis (Pilleri and Gihr, 1972)	X	X
N. phocaenoides sunameri (Pilleri and Gihr, 1975)	X	X
Phocoena phocoena phocoena (Linnaeus, 1758)	X	X
P. phocoena vomerina Gill, 1856	X	X
P. phocoena relicta Abel, 1905	X	X
***P. phocoena* subsp. (un-named) [Western North Pacific]**		
Phocoenoides dalli dalli (True, 1885)***	X	X
P. dalli truei Andrews, 1911	X	X

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