



Taxonomic revision of the dolphin genus *Lagenorhynchus*

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ABSTRACT

Evolutionary relationships among cetaceans within the family Delphinidae have been difficult to resolve due to the high number of species and their relatively rapid radiation. This is the case for the dolphin species currently placed in the genus *Lagenorhynchus*, and their relations to *Cephalorhynchus* and *Lissodelphis* species. Phylogenetic relationships among these species have been investigated using multiple lines of evidence, and that evidence consistently suggests that the six species currently assigned to *Lagenorhynchus* do not form a monophyletic group. Here, we summarize findings from studies of morphology, genetics, historical biogeography, and acoustics that offer insight into the phylogenetics of these taxa. We present the taxonomic basis for revision of *Lagenorhynchus*, propose retention of *Lagenorhynchus albirostris* and reassignment of the remaining five species into other existing generic names, namely *Leucopleurus acutus*, *Sagmatias australis*, *Sagmatias cruciger*, *Sagmatias obliquidens*, and *Sagmatias obscurus*. Making these revisions now so that the taxonomy better reflects evolutionary relationships among these species will ensure that future studies include the most appropriate taxa for investigating the

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complex phylogenetic and systematic relationships among cetaceans. However, comprehensive analyses using multiple lines of evidence are still needed to clarify the phylogenetic relationships within and among the Lissodelphininae genera *Cephalorhynchus*, *Lissodelphis*, and *Sagmatias*.

Key words: *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, Lissodelphininae, *Lissodelphis*, phylogenetics, *Sagmatias*, systematics, taxonomy.

Unraveling the systematic relationships among the world's dolphin species has been a contentious undertaking since Linnaeus first assigned species as disparate as killer whales, common dolphins, and harbor porpoises to a single genus, *Delphinus*, in 1758. The decision to assign dolphin species to a single large group was likely due to a tradition of taxonomic classification guided by similarities in internal and external morphological characteristics (e.g., skulls and skeletal elements, tooth count, pigmentation). The modern formulation of this idea is that the presence of shared derived characters ("synapomorphies") links species with close evolutionary relationships (Hennig 1966). However, relatively recent advances in the field of molecular genetics have revealed that morphological similarities can sometimes be deceiving. Application of DNA evidence is now challenging traditional, morphology-based taxonomy and improving our understanding of evolutionary relationships among marine mammals.

With respect to the taxonomy of cetaceans (members of Cetacea—an unranked taxon within the order Cetartiodactyla), there has been considerable discussion recently concerning classification at the species and subspecies levels (e.g., *Tursiops* and *Stenella*: Perrin *et al.* 2013; *Balaenoptera*: Wada *et al.* 2003, Archer *et al.* 2013, Rosel and Wilcox 2014; *Sousa*: Mendez *et al.* 2013, Jefferson and Rosenbaum 2014; *Delphinus*: Cunha *et al.* 2015; *Orcinus*: Morin *et al.* 2010), and mounting evidence indicates that reclassification is needed at higher taxonomic levels as well (e.g., see discussion of genus-level revisions in Perrin *et al.* 2013). Classification has been particularly challenging when it comes to highly speciose families such as Delphinidae (LeDuc *et al.* 1999, Perrin *et al.* 2013), for which 37 species are currently listed by the Society for Marine Mammalogy's Committee on Taxonomy (2018). The sheer number of dolphin species, in addition to their rapid and relatively recent radiation (e.g., Kingston *et al.* 2009, LeDuc *et al.* 1999, Steeman *et al.* 2009, McGowen 2011, Perrin *et al.* 2013), has made genus-level taxonomy within the family Delphinidae difficult to resolve.

Among the delphinids, classification of the species within the genera *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* is particularly challenging. These three genera have generally been considered to be close relatives and they have been grouped within the subfamily Lissodelphininae since LeDuc *et al.* (1999) used molecular data to investigate the phylogenetic relationships within the Delphinidae (detailed below). *Cephalorhynchus* includes four small-bodied, blunt-headed species (*C. commersonii*, *C. eutropia*, *C. heavisidii*, *C. hectori*) found in inshore

or coastal waters of the Southern Hemisphere. *Lissodelphis* includes two offshore species (*L. borealis*: northern Pacific; *L. peronii*: circumpolar in Southern Hemisphere) exhibiting an elongated and streamlined body shape with a distinct rostrum and no dorsal fin. *Lagenorhynchus* includes six species, three inhabiting offshore and coastal waters of the Northern Hemisphere (*L. acutus* and *L. albirostris* in the Atlantic; *L. obliquidens* in the Pacific) and the remaining three in offshore (*L. cruciger*), inshore, and coastal (*L. australis*, *L. obscurus*) waters of the Southern Hemisphere (Fig. 1).

No species of *Lagenorhynchus*, *Cephalorhynchus*, or *Lissodelphis* is currently well-represented, if represented at all, in the fossil record. The oldest known occurrence of the Delphinidae is a skull from about 10–11 Ma (mega-annum; Barnes 1977). A Late Pleistocene skull assigned to the genus *Lagenorhynchus* (but not to a particular species) was collected from the Palos Verdes Sand Formation (ca. 120,000 yr ago) in Newport Bay, California (Barnes 1977). The only other fossils assigned to *Lagenorhynchus* are *L. harmatuki*, described from a cranium discovered in the Yorktown Formation (ca. 4.8–3.1 Ma in the Early Pliocene) at Lee Creek Mine, North Carolina, and two petrosals and several teeth described as *Lagenorhynchus* sp. likely also from the Yorktown Formation (Snyder *et al.* 1983, Whitmore and Kaltenbach 2008). To date, no *Cephalorhynchus* or *Lissodelphis* fossils have been described.

Although members of *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* are quite distinct based on morphological differences, such as body shape, skull features/characteristics, and coloration, studies using genetic data have revealed that the phylogenetic relationships among them are much less clear and suggest that some taxonomic revision is needed (LeDuc *et al.* 1999, Harlin-Cognato and Honeycutt 2006, McGowen 2011, Banguera-Hinestroza *et al.* 2014a). For *Lagenorhynchus* specifically, numerous studies (discussed below; Table 1) have described the paraphyletic nature of this genus.

To date, no taxonomic changes have been formally proposed or accepted, although some publications have used the “next available” names that were informally suggested by LeDuc *et al.* (1999). To this end, a workshop entitled “Rethinking *Lagenorhynchus*” was held at the 21st Biennial Conference on the Biology of Marine Mammals (San Francisco, California, December 2015) and focused on *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis*. The main workshop goals were to better understand the current state of knowledge regarding classification of species within and among these genera, and to identify additional information and resources needed to support any taxonomic revisions. The main objectives of this paper are to (1) synthesize the information presented during discussions arising from the workshop as it pertains to reclassification of the six species currently assigned to *Lagenorhynchus*, (2) consider their relationship to *Cephalorhynchus* and *Lissodelphis*, and (3) present the evidence in support of formal taxonomic revision. We (1) summarize available data on morphology, genetics, historical biogeography, acoustics, and other potentially relevant factors to advance efforts to revise the genus-level taxonomy of the species currently

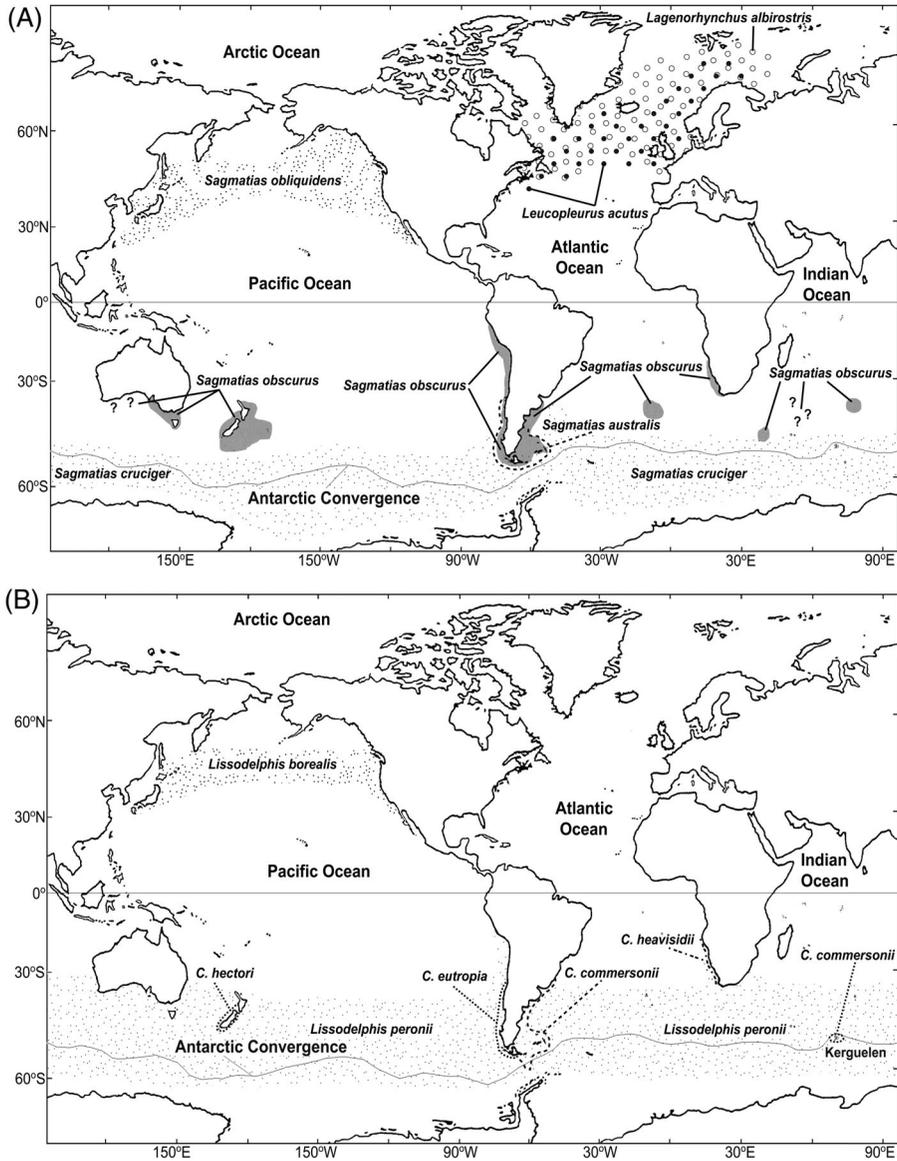


Figure 1. Distribution of (A) *Lagenorhynchus*, *Leucopleurus*, and *Sagmatias* species, and (B) *Cephalorhynchus* and *Lissodelphis* species. Unconfirmed sightings of *S. obscurus* off southwestern Australia and in the southern Indian Ocean are depicted by “?”.

assigned to *Lagenorhynchus*; (2) summarize phylogenetic affinities currently supported by multiple lines of evidence; (3) present a formal taxonomic treatment and revision of *Lagenorhynchus*; and (4) highlight data gaps and avenues for future research.

Table 1. Genetic (GEN) and morphological (MOR) research that includes *Lagenorhynchus*, *Cephalorhynchus*, and/or *Lissodelphis* species (as currently named) in either focused or broad-scale analysis of taxonomic and/or phylogenetic relationships. Species presence (✓) or absence (—) is denoted for each set of references.

	Lacu	Lalb	Laus	Lcru	Lobl	Lobs	Ccom	Ceut	Chea	Chec	Libor	Liper	GEN data used?	MOR data used?	Reference
✓	—	✓	—	✓	✓	✓	—	—	—	—	—	—	no	yes	Fraser 1966
✓	✓	—	✓	—	✓	✓	—	—	✓	✓	✓	—	no	yes	Mead 1975
✓	✓	✓	—	✓	✓	✓	*	*	*	*	✓	✓	no	yes	de Muizon 1988
✓	✓	—	—	—	✓	✓	✓	—	—	✓	—	✓	yes	no	Cipriano 1997
✓	✓	✓	✓	✓	✓	✓	—	—	—	—	—	—	no	yes	Miyazaki and Shikano 1997b
—	✓	—	—	—	—	✓	—	✓	—	—	✓	✓	yes	no	Messenger and McGuire 1998
✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	yes	no	LeDuc et al. 1999, Harlin-Cognato and Honeycutt 2006, Steeman et al. 2009, McGowen et al.
✓	✓	—	—	—	—	—	—	—	—	—	—	—	no	yes	2009, McGowen 2011, Banguera-Hinestroza et al. 2014a
✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	—	✓	yes	no	Pichler et al. 2001
✓	✓	—	—	—	✓	✓	—	—	—	✓	✓	—	no	yes	Buchholtz and Schur 2004
✓	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	yes	no	May-Collado and Agnarsson 2006, Agnarsson and May-Collado 2008
—	—	✓	—	—	—	—	✓	✓	—	—	—	—	yes	no	Caballero et al. 2008
✓	✓	✓	—	—	✓	✓	✓	✓	✓	✓	✓	✓	no	yes	Moreno 2008
✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	—	yes	no	Slater et al. 2010
—	✓	—	—	—	—	—	—	—	—	—	—	—	yes	no	Vilstrup et al. 2011
✓	✓	✓	—	—	—	—	—	—	✓	✓	✓	—	yes	yes	Murakami et al. 2014
✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	no	yes	Galatius and Goodall 2016

Abbreviations: *L. acutus* (Lacu), *L. albirostris* (Lalb), *L. australis* (Laus), *L. cruciger* (Lcru), *L. obliquidens* (Lobl), *L. obscurus* (Lobs), *C. commersonii* (Ccom), *C. eutropia* (Ceut), *C. beavisidii* (Chea), *C. hectori* (Chec), *L. borealis* (Libor), *L. peronii* (Liper).

*In de Muizon (1988) it is not clear which species were used for analyses (e.g., fig. 30, p. 215), list of species names here are taken from fig. 33, p. 219.

AVAILABLE DATA

Morphological Evidence

Here we present morphological evidence based on analysis of skull and postcranial characters, and later under *Acoustic Evidence* we discuss morphological differentiation in relation to sound production. Relatively few studies have investigated the morphological evidence useful for reconstructing evolutionary relationships of the six currently recognized *Lagenorhynchus* species (Table 1). Even fewer studies have analyzed a complete data set that includes all *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species. Nonetheless, the morphological data examined suggest paraphyly of the species currently assigned to *Lagenorhynchus*, and even the earliest naturalists working on marine mammal taxonomy raised concerns about the validity of this genus as currently described. For example, obvious morphological differences prompted Gray (1868b) to suggest that *Lagenorhynchus albirostris* (the type species for the genus) and *Leucopleurus arcticus* (a synonym of *Lagenorhynchus acutus*) each be assigned to its own monotypic genus. Subsequently, Flower (1884) noted the variability of the skull morphology within *Lagenorhynchus*, particularly mentioning *L. albirostris* and *L. acutus* as being well-differentiated from the other species. More recently, Fraser (1966) compared pigmentation patterns and cranial features and included focused descriptions of *L. australis*, *L. cruciger*, and *L. obscurus* specimens. He described close similarities between *L. australis* and *L. cruciger* based on cranial measurements in relation to condylobasal length, and particularly noted their distinctiveness from *L. obscurus*, concluding that “placing of the dusky dolphin [*L. obscurus*] in the genus *Lagenorhynchus* is still dubious.”

Using data from all six *Lagenorhynchus* species (but with no “out-groups”—representatives of other lineages), Miyazaki and Shikano (1997b) conducted a morphology-based classification using canonical discriminant analysis of 20 cranial measurements, and distinct morphological differences were found among all species. Additional analysis using Mahalanobis’ generalized distance revealed that *L. obliquidens* clustered with *L. obscurus*, *L. australis* clustered with *L. cruciger*, and all four species clustered closer to *L. acutus* than to *L. albirostris* (Miyazaki and Shikano 1997b).

Moreno (2008) also used morphological characters in a phylogenetic analysis of 43 taxa in the family Delphinidae and included in that analysis 1–3 specimens from all *Lagenorhynchus* (except *L. cruciger* for which material was unavailable), *Cephalorhynchus*, and *Lissodelphis* species. Using 147 characters (from skull measurements, tympano-periotic bones, external morphology, and color patterns), Moreno (2008) found support for the distinctiveness of *L. acutus* and *L. albirostris*, both from each other and from all other *Lagenorhynchus* species, and support for placing *L. acutus* within the Delphininae, with *L. albirostris* in a new, monotypic subfamily Lagenorhynchinae. Support was also found for grouping the remaining *Lagenorhynchus* species along with those of *Cephalorhynchus* and *Lissodelphis* into the subfamily Lissodelphininae (*sensu*

LeDuc *et al.* 1999). From his parsimony-based analysis, Moreno posited a close relationship between *L. obliquidens* and *L. obscurus*, and between *L. australis* and the four *Cephalorhynchus* species, and proposed reassignment of *L. australis* and *L. cruciger* to *Cephalorhynchus* (although he had no specimens of *L. cruciger* to examine and relied on morphological and acoustic analyses by other authors to support a sister-species relationship between *L. australis* and *L. cruciger*). However, apart from differences in coloration, only “non-exclusive morphological synapomorphies” supported Moreno’s proposed groupings, *i.e.*, characters were unique only when comparing species of Lissodelphininae (*sensu* LeDuc *et al.* 1999) and not when including comparisons with other taxa outside of this subfamily.

Genetic Evidence

The explosive growth in the availability of genetic data has shed additional light on the problematic systematics of the genus *Lagenorhynchus* (Table 1). Results from genetic analyses parallel those from morphology-based analyses and lead to a common conclusion that *Lagenorhynchus* is not monophyletic. As with the morphological studies, few of the molecular genetic studies of phylogenetic relationships have incorporated data from all six *Lagenorhynchus* species and their *Cephalorhynchus* and *Lissodelphis* relatives, with material from *L. peronii* and, importantly, *L. cruciger* often absent from genetic data sets. Below, we briefly review genetic studies that have used data from multiple species from the three focal genera to gain insight into the evolutionary relationships among these taxa. We emphasize that it is important to be aware of the data used (*i.e.*, one gene or many genes, nuclear and/or mitochondrial data, breadth of taxonomic sampling, *etc.*) when interpreting any phylogenetic reconstruction (*e.g.*, Maddison 1997, Nichols 2001, Degnan and Rosenberg 2009, Yang and Rannala 2012).

The earliest genetic work on *Lagenorhynchus* phylogenetics investigated the relationships among *L. acutus*, *L. albirostris*, *L. obliquidens*, and *L. obscurus* using DNA sequence data from two commonly used mitochondrial regions: the control region (mtCR) and the cytochrome *b* gene (*cyt-b*; Cipriano 1997). Net nucleotide sequence divergence (Jukes-Cantor corrected) was lowest between *L. obliquidens* and *L. obscurus* (mtCR = 5.20%, *cyt-b* = 2.71%), and highest in all comparisons with *L. acutus* (mtCR = 5.17%–7.38%, *cyt-b* = 8.44%–9.78%) and *L. albirostris* (mtCR = 7.38%–13.02%, *cyt-b* = 8.46%–10.30%). Although Taylor *et al.* (2017) provided sequence divergence thresholds helpful for delimiting cetacean species, subspecies, and populations, there are no established thresholds for divergence estimates by which higher-level taxonomic units (*i.e.*, genus-level) are judged. The same four *Lagenorhynchus* species were also analyzed, along with mtCR and/or *cyt-b* sequence data from other delphinid (*e.g.*, *Cephalorhynchus hectori*, *C. commersonii*, *Delphinus delphis*, *Orcinus orca*, *Stenella longirostris*) and outgroup taxa (*e.g.*, *Phocoena phocoena*, *Balaenoptera physalus*), using maximum parsimony (MP) analysis. For phylogenetic reconstructions

using mtCR data, there was no resolution among any of the delphinid taxa (*i.e.*, there were no multispecies clades with a bootstrap value ≥ 70). However, reconstructions based on *cyt-b* data did produce moderate support (bootstrap ≥ 80) for a clade grouping together *Stenella* and *Delphinus* species, as well as a clade containing all *L. obliquidens* and *L. obscurus*. All *L. acutus* and *L. albirostris* grouped neither with any other species nor with each other. Taken together, the findings of Cipriano (1997) support a relatively close genetic relationship between *L. obliquidens* and *L. obscurus*, with *L. acutus* and *L. albirostris* being only distantly related. This was the first genetic study supporting the hypothesis that the species within *Lagenorhynchus* do not form a monophyletic group.

LeDuc *et al.* (1999) conducted the first comprehensive, and widely cited, phylogenetic analysis involving representatives from all *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species. This study used complete *cyt-b* sequences (1,140 base pairs or bp) from at least one individual per species representing 32 delphinid species. A well-supported (both Neighbor Joining (NJ) and parsimony bootstrap values = 100) consensus tree provided statistical support for the grouping of the four *Cephalorhynchus*, two *Lissodelphis*, and four of the *Lagenorhynchus* species together, to the exclusion of *L. albirostris* and *L. acutus* (Fig. 2A). Based on these findings, LeDuc *et al.* (1999) suggested Lissodelphininae as the subfamily name for this 10-species cluster since the type species of *Lagenorhynchus* (*i.e.*, *albirostris*) clustered outside of this group. This expanded the subfamily Lissodelphininae from its original monotypic status (type genus *Lissodelphis*) established by Fraser and Purves (1960).³ Furthermore, LeDuc *et al.* (1999), based on results from a single molecular marker, introduced two oft-reiterated hypotheses regarding *Lagenorhynchus* and Lissodelphininae: (1) *L. acutus* and *L. albirostris* are neither closely related to the other four *Lagenorhynchus* species, nor to each other; and (2) the relationships within Lissodelphininae are not well-resolved. Because *L. albirostris* is the type species for *Lagenorhynchus*, LeDuc *et al.* (1999) suggested that a future revision might resurrect *Leucopleurus* (originally proposed as a subgenus of *Lagenorhynchus* by Gray 1866b) as the “next available” generic name for *acutus*, and that *Sagmatias* Cope, 1866 was the “next available” genus name most appropriate for the remaining four *Lagenorhynchus*⁴ species (with *australis* as the type species).

More recently, three genetic analyses (May-Collado and Agnarsson 2006, Agnarsson and May-Collado 2008, Slater *et al.* 2010) included the published *cyt-b* sequences from LeDuc *et al.* (1999), incorporated increased representation outside of the Delphinidae (*i.e.*, extensive genetic sampling of the Cetartiodactyla), and used either maximum likelihood (ML) or Bayesian analyses to investigate phylogenetic relationships. These studies

³Fraser and Purves (1960) used mainly the morphology of the air sinuses to recognize several new subfamilies within the family Delphinidae, including Lissodelphininae. Rice (1984, 1998) corrected the spelling of Lissodelphininae to Lissodelphininae.

⁴Throughout the remaining text, tables, and figures, except for the Knowledge Gaps and Future Research section, Figure 1, and Table S1, we continue to use *Lagenorhynchus* to refer to these four species rather than cumbersome formulations such as “the species formerly known as *Lagenorhynchus*.”

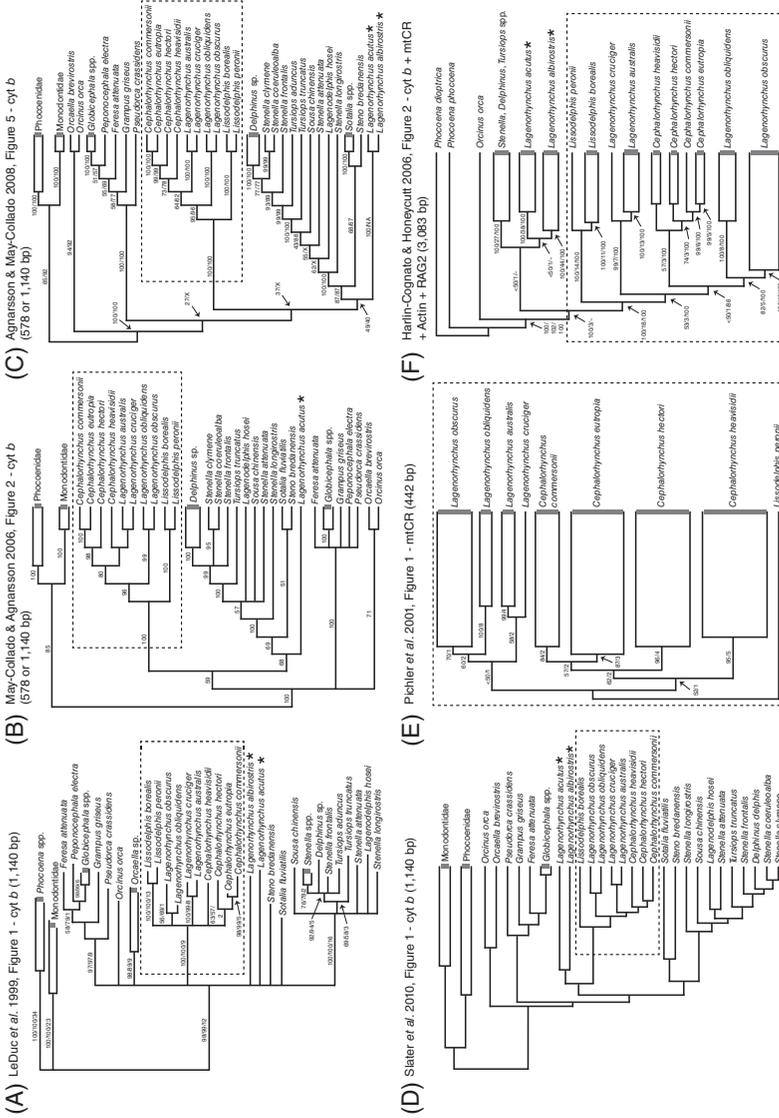


Figure 2. Reproductions of phylogenetic reconstructions originally built using mitochondrial cytochrome *b* (cyt-*b*), mitochondrial control region (mtCR), and nuclear DNA data (Actin, RAG2). Dashed boxes highlight *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species (as currently named), asterisks denote *L. acutus* and *L. albirostris* when present in analyses, vertical gray bars denote clades representing multiple species or as in (E) and (F) multiple specimens per species. The total number of base pairs (bp) reported for each study is given. (A) Parsimony bootstrap/neighbor joining bootstrap/Bremer index values shown. (B) Posterior probabilities shown. (C) Posterior probabilities for full/pruned data sets shown; “N/A” denotes index values that were not tested in pruned data set; “X” denotes clades recovered in full but rejected in pruned data set; *L. albirostris*, although present in the tree, was not included in analyses. For both (B) and (C), all sequences were 1,140 bp except some included in Phocoenidae that were 578 bp. (D) No support values given in original publication. (E) Parsimony bootstrap/Bremer index values shown. (F) Parsimony bootstrap/decay index/posterior probability values shown; “~” denotes no value given in original publication.

also found *Lagenorhynchus* to be a paraphyletic group and recovered a monophyletic group (*i.e.*, Lissodelphininae *sensu* LeDuc *et al.* 1999) including *Cephalorhynchus*, *Lissodelphis*, and the four *Lagenorhynchus* species (Fig. 2B–D).

Pichler *et al.* (2001) focused on reconstructing the evolutionary histories of the genus *Cephalorhynchus*. These authors used data from either 390 bp or 442 bp of the mtCR, robust sampling within *Cephalorhynchus* (20–200 individuals per species), 1–2 individuals for all *Lagenorhynchus* and *Lissodelphis* species (excluding *L. borealis*), and numerous other Delphinidae species as outgroups for initial analyses. In these initial analyses (not shown in Pichler *et al.* 2001), the authors found no support for a close relationship between the nine Lissodelphininae species (*sensu* LeDuc *et al.* 1999 and excluding *L. borealis*) and *L. acutus* or *L. albirostris*. In subsequent MP and NJ analyses using only the nine Lissodelphininae species, two distinct but weakly supported monophyletic *Cephalorhynchus* and *Lagenorhynchus* clades were recovered (Fig. 2E). These authors also found a diagnostic insertion-deletion event (indel)—in this case a deletion from 5 to 22 bp long (length depending on the species)—present only in *Cephalorhynchus*, and two “fixed” and diagnostic nucleotide substitutions (between *Cephalorhynchus* and the four *Lagenorhynchus* species analyzed) that further support a monophyletic *Cephalorhynchus* clade. The appropriate weighting for use of indels as a diagnostic character for taxonomic discrimination has not been determined and, because sequence-based phylogenetic analysis methods are typically focused on substitution events (Ashkenazy *et al.* 2014), use of this potentially highly-informative character was not included in the Pichler *et al.* (2001) analysis or in any of the subsequent analyses mentioned below. Other cetacean genera similarly have relatively large (≥ 5 bp) indels within the mtCR that provide diagnostic differences both among species within a genus (*e.g.*, *Phocoena* species: Rosel *et al.* 1995; *Mesoplodon*: Dalebout *et al.* 2004) and among genera (*e.g.*, family Ziphiidae: Dalebout *et al.* 1998).

While these studies have consistently shown *Lagenorhynchus* to be a paraphyletic assemblage, all but Cipriano (1997) and Pichler *et al.* (2001) were based largely on the same set of genetic specimens, and essentially a single mitochondrial gene (LeDuc *et al.* 1999, May-Collado and Agnarsson 2006, Agnarsson and May-Collado 2008, Slater *et al.* 2010). Use of maternally inherited mitochondrial markers and biparentally inherited nuclear markers, as well as incorporation of multiple loci and/or gene regions (both coding and noncoding), is important to gain an accurate depiction of genetic variability and phylogenetic relationships at higher taxonomic levels. As such, the studies summarized below aimed to strengthen existing data sets by incorporating analyses of multiple molecular markers and gene regions.

Harlin-Cognato and Honeycutt (2006) incorporated data from two mitochondrial regions (complete *cyt-b* and partial mtCR), two nuclear genes (Actin and RAG2), and multiple individuals for most species⁵ in a

⁵Data from a single individual was used for each of *L. cruciger*, *C. eutropia*, and *L. peronii*. However, no data were analyzed for the Actin gene in these three species or for RAG2 in *C. eutropia*.

study focused on resolving relationships among *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis*. Results based on both MP and Bayesian analyses included: high support for the grouping of Lissodelphininae (*sensu* LeDuc *et al.* 1999) with *L. acutus* and *L. albirostris* excluded, low support for *L. acutus* and *L. albirostris* clustering together, and low support for a close relationship of *L. acutus* or *L. albirostris* with other delphinid genera (*e.g.*, *Stenella*, *Delphinus*, *Tursiops*; Fig. 2F). Within the Lissodelphininae clade, Harlin-Cognato and Honeycutt's (2006) analysis showed close associations between (1) the two *Lissodelphis* species, (2) *L. australis* and *L. cruciger*, (3) *L. obscurus* and *L. obliquidens*, and (4) all four *Cephalorhynchus* species (Fig. 2F). There was also high support for *Lissodelphis* as a sister group to the other three lineages listed above, but no resolution of relationships among those three lineages (Fig. 2F, Harlin-Cognato and Honeycutt 2006). Although Harlin-Cognato and Honeycutt (2006) did include data from the mtCR in analyses, they did not attempt to include the "diagnostic" (Pichler *et al.* 2001) control region indel in their Bayesian analysis. Overall, although some lineages (shown in Fig. 2F) had MP bootstrap proportions well below the minimum acceptable threshold of 70% (Hillis and Bull 1993), this study was robust in that it had increased taxonomic sampling (multiple individuals per species and species per genus), used both nuclear and mitochondrial markers, and performed various statistical analyses to produce phylogenetic reconstructions.

In a subsequent phylogenetic analysis, Steeman *et al.* (2009) attempted to resolve relationships among all extant cetaceans and recovered a clade that included *C. beavisidii* grouped with *L. australis*, *L. cruciger*, *L. obliquidens*, and *L. obscurus*, and separate from a clade of the remaining *Cephalorhynchus* species. The tree in that analysis was constructed within a Bayesian analytical framework using published genetic data from six mitochondrial regions (but no mtCR data) and nine nuclear genes. However, the considerable amount of missing data for *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* (7/12 and 12/12 species had >50% missing for mitochondrial and nuclear data, respectively) suggests that these results should be regarded with some caution.

McGowen (2011) used both previously published and newly acquired genetic data and in total combined information from four mitochondrial regions (study included no mtCR data) and 20 nuclear genes in a large-scale study focused on resolving the phylogeny of Delphinidae.⁶ This work included data from at least one individual for all *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species (two each of *C. commersonii* and *L. borealis*). McGowen (2011) found differing topologies involving the three focal genera depending on which gene sequences (nuclear data only, mitochondrial data only, or combined nuclear and mitochondrial data) were used to build the trees (using either Bayesian or ML methods). For example, all phylogenies supported the paraphyly of *Lagenorhynchus*, the grouping of Lissodelphininae (*sensu* LeDuc *et al.*

⁶The study by McGowen (2011) supplemented the data set analyzed in earlier work by McGowen *et al.* (2009). Because the more recent study is based on a more complete genetic data set the details of McGowen *et al.* (2009) are not discussed in detail here.

1999), and both *L. acutus* and *L. albirostris* as sister taxa of the family Delphinidae (Fig. 3A–C). However, the analysis using mitochondrial data only showed support for the groupings of *C. commersonii* and *C. eutropia* with *C. hectori*, *L. australis* with *L. cruciger*, *L. obliquidens* with *L. obscurus*, and *Lissodelphis* as a sister group to all *Cephalorhynchus* and *Lagenorhynchus* species (Fig. 3A). Using nuclear data,

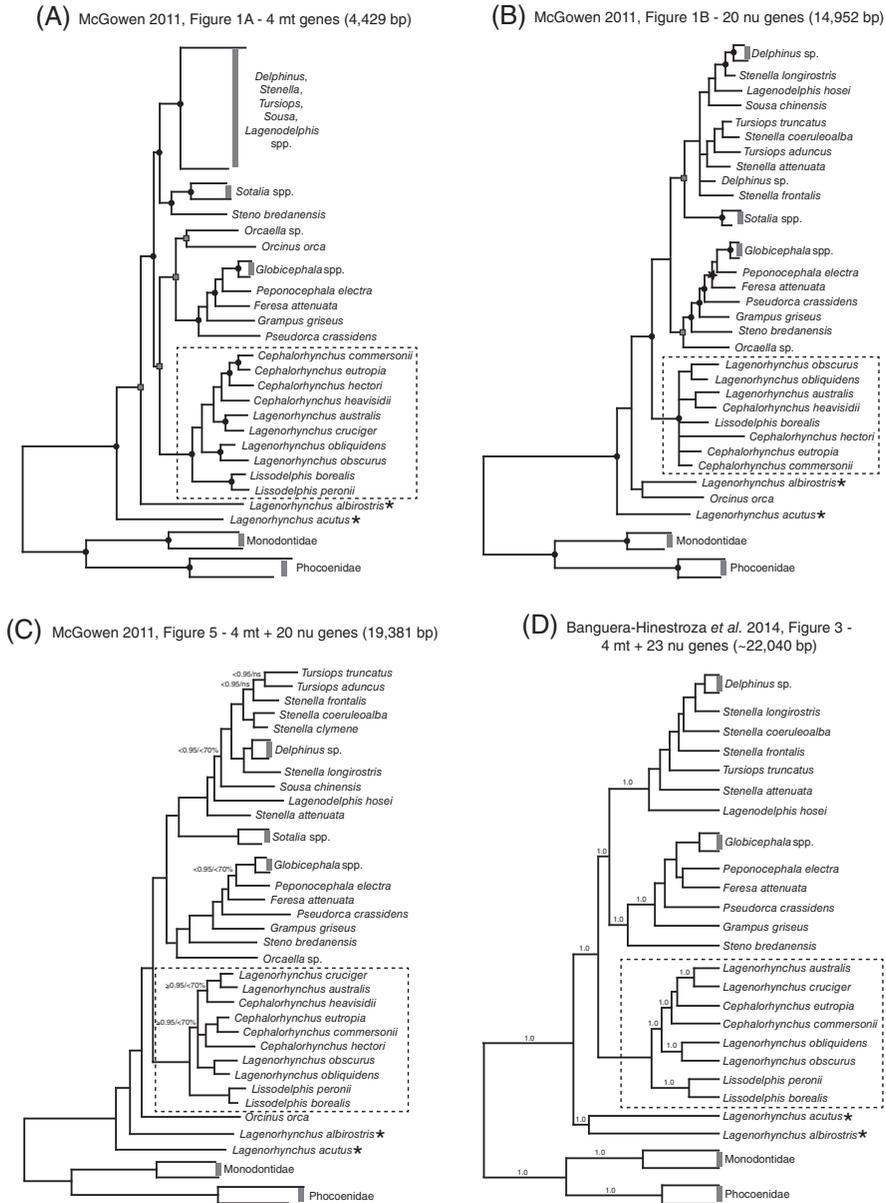


Figure 3. Legend on next page.

Table 2. Missing data in two recent molecular phylogenetic studies. The number of markers used in analyses, per species, are shown.

	McGowen 2011		Banguera-Hinestroza <i>et al.</i> 2014a	
	Targeted total: 4 mt and 20 nu		Targeted total: 4 mt and 23 nu	
	# mt analyzed	# nu analyzed	# mt analyzed	# nu analyzed
Ccom	4	20	4	23
Ceut	3	5	3	6
Chea	1	1	NA	NA
Chec	1	2	NA	NA
Libor	4	19	4	18
Liper	3	0	3	0
Lacu	4	19	4	22
Lalb	4	19	4	21
Laus	1	5	2	9
Lcru	1	0	2	5
Lobl	4	20	4	23
Lobs	4	17	4	20

Abbreviations: Species abbreviations are the same as Table 1; mitochondrial markers (mt); nuclear markers (nu); species not included in study (NA).

McGowen (2011) found that relationships are statistically unresolved beyond the clustering of LeDuc *et al.*'s Lissodelphininae species within a single clade (Fig. 3B). It is worth noting that among the species from the three focal genera, 6 of 12 were missing at least 50% of the nuclear data for analyses, while 4 of 12 were missing at least 50% of the mitochondrial data (Table 2). A majority consensus phylogram of combined nuclear and mitochondrial data largely mirrors that of the mitochondrial tree (Fig. 3C).

Banguera-Hinestroza *et al.* (2014a) focused on biogeography and divergence times of the extant Delphinoidea (Monodontidae, Phocoenidae, Delphinidae) using previously published (including data from McGowen 2011) and newly acquired genetic data, and in total combined information from four mitochondrial regions (same four as

Figure 3. Reproductions of recent phylogenetic reconstructions built using numerous mitochondrial (mt) and nuclear (nu) genes. Dashed boxes highlight *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species (as currently named), asterisks denote *L. acutus* and *L. albirostris*, vertical gray bars denote clades representing multiple species. The total number of base pairs (bp) reported for each analysis is given. (A) and (B) Black dots denote nodes with maximum likelihood bootstrap (ML) $\geq 70\%$ and Bayesian posterior probability (PP) ≥ 0.95 , grey squares denote only ML $\geq 70\%$, black star denotes only PP ≥ 0.95 . (C) All nodes have PP ≥ 0.95 and ML $\geq 70\%$ unless otherwise shown (PP/ML), "ns" denotes no support for that analysis. (D) PP values shown, only nodes with PP of 1.0 were denoted in original publication, the total bp was not reported for this study, therefore an approximation was calculated by averaging the total bp gathered from the GenBank files for the five species with no missing data across all 27 genes.

McGowen 2011; study included no mtCR data) and 23 nuclear genes. This study included data from all *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species, except for *C. beavisidii* and *C. hectori*. Multiple individuals were amplified and analyzed for some species; however, the authors noted that there was no difference in tree topology if one or multiple individuals per species were used (Banguera-Hinestroza *et al.* 2014a). The supermatrix tree of combined mitochondrial and nuclear data found a close relationship between *L. australis* and *L. cruciger*, however, these species grouped within a clade containing *C. commersonii* and *C. eutropia* (Fig. 3D). The clustering together of these four species is likely influenced by the exclusion of genetic data from both *C. beavisidii* and *C. hectori*. A close relationship was recovered between *L. obliquidens* and *L. obscurus* and separately between the two *Lissodelphis* species. Altogether, a monophyletic clade representing LeDuc *et al.*'s (1999) Lissodelphininae was recovered, with *L. acutus* and *L. albirostris* as a sister group of all other delphinids in this study (Fig. 3D). Among the species from the three focal genera (recognizing that *C. beavisidii* and *C. hectori* were not included in any data set), 4 of 10 were missing at least 50% of the nuclear data for analyses and 2 of 10 were missing at least 50% of the mitochondrial data (Table 2).

Overall, there have been numerous attempts using genetic data to resolve the phylogenetic relationships among the species of *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis*. Taken together, the genetic data support the paraphyly of *Lagenorhynchus* and the relatively distant relationships of *L. acutus* and *L. albirostris*; however, additional sampling of genetic data from some species (*e.g.*, *L. cruciger*) and more consistent genetic sampling across all species (*i.e.*, less missing data) are needed to resolve the finer-scale taxonomic relationships of this group.

Historical Biogeographical Evidence

The species currently assigned to *Lagenorhynchus* and *Lissodelphis* have a distinctively antitropical distribution and inhabit coastal and offshore waters in both the Northern and Southern Hemispheres (Fig. 1). The *Cephalorhynchus* species occur only in temperate latitudes of the Southern Hemisphere, mainly along the coasts of southern South America, southwestern Africa, New Zealand, and the Falkland and Kerguelen Islands (Fig. 1B). Exploring the geographical distribution of these species over space and time might provide a better understanding of the evolutionary relationships among them. Much of the support for historical biogeographical patterns among dolphins has been based on genetic data. Therefore, we include here previously mentioned studies but we discuss results in terms of biogeography and divergence times rather than strictly genetic relatedness.

The common ancestor of the family Delphinidae is hypothesized to have originated within the North Atlantic prior to or during the middle Miocene (Banguera-Hinestroza *et al.* 2014a). Of the two descendants of this ancestor, one diverged into the common ancestor of *L. acutus* and *L. albirostris* around 11.49 Ma, and the other evolved into the remaining delphinids, including LeDuc *et al.*'s (1999) Lissodelphininae, around 10.29 Ma (Banguera-Hinestroza *et al.* 2014a). The remaining *Lagenorhynchus*,

Cephalorhynchus, and *Lissodelphis* species possibly diverged around 5.31 Ma within the Southern Hemisphere, with subsequent dispersions northward in the Pacific for *L. borealis* and *L. obliquidens* (Banguera-Hinestroza et al. 2014a). A common ancestor for *L. australis*, *L. cruciger*, *C. commersonii*, and *C. eutropia* in the Southern Hemisphere around 3.5 Ma was suggested by Banguera-Hinestroza et al. (2014a). Estimates from multiple studies place the divergence between *L. obscurus* and *L. obliquidens* most recently at around 2 Ma (Cipriano 1997, Harlin-Cognato et al. 2007, Banguera-Hinestroza et al. 2014a), although these studies disagree on whether the dispersal/speciation event in the Pacific was from south to north or *vice versa*. During the Neogene (23–2.6 Ma), changes in both climatic and oceanographic characteristics correlate to the diversification of delphinids in both the Northern and Southern Hemisphere (e.g., Gaskin 1976, Fordyce 1989, Whitmore 1994). Overall, the early divergence and North Atlantic distribution of both *L. acutus* and *L. albirostris* support their differentiation from the remaining four *Lagenorhynchus* species. Furthermore, the more recent Southern Hemisphere origin for *L. australis* and *L. cruciger*, and possibly also for *L. obliquidens* and *L. obscurus*, provides support for the close evolutionary relationships among these species.

Acoustic Evidence

Acoustic signals of some birds, mammals, amphibians, and insects have effectively addressed taxonomic questions when the specific components of signals that are taxonomically informative are known (e.g., Anderson et al. 2000, Gray and Cade 2000, Irwin et al. 2001, Ryan et al. 2007). Acoustic signals produced by odontocetes include three call types: (1) echolocation clicks for navigation and prey finding; and for communication: (2) burst-pulse calls and (3) whistles (Richardson et al. 1995). The call types produced by a given species, and the spectral and temporal features of echolocation clicks that correspond to sound production morphology, are often conserved within odontocete families and may reflect evolutionary divergence (Cranford et al. 1996, May-Collado et al. 2007, Morisaka and Connor 2007, Baumann-Pickering et al. 2013). Therefore, we review what is known about odontocete sound production morphology and how it relates to temporal and spectral features of echolocation clicks as well as the production of whistles, with a focus on *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis*.

The evolution of sound production morphology in odontocetes has varied across taxa, with homologous structures influencing the temporal and spectral characteristics of the echolocation clicks that are produced (Cranford et al. 1996, Cranford and Amundin 2004, McKenna et al. 2012). Briefly, echolocation clicks are generated at a single pair (only in Physteridae and Kogiidae) or a double pair of bursae complexes (also known as the monkey lip dorsal bursae complex or phonic lips) within the nasal air passages, and are focused into a narrow beam that propagates out to the external environment *via* complex interactions with the skull, air sacs, and acoustic lipid structures, such as the melon, in the “forehead” (Cranford et al. 1996). Although some mechanisms of odontocete click

production remain unclear (e.g., Cranford *et al.* 2011, Madsen *et al.* 2013), it is known that features of the sound generators and sound propagation anatomy, such as the number of bursae complexes, and the locations, relative positions, sizes, shapes, and material composition of the bursae complexes and forehead anatomy, affect the resonance frequencies and can determine the frequency content of the echolocation clicks that are produced (Amundin and Cranford 1990, Cranford and Amundin 2004). Genera with a single bursae complex (*Physeter* and *Kogia*) or two nearly symmetrical bursae complexes (e.g., *Phocoena*, *Cephalorhynchus*) tend to produce clicks with a narrow frequency bandwidth, a unimodal peak in the frequency spectrum, and a long-duration, polycyclic waveform (Cranford and Amundin 2004, Morisaka and Connor 2007, Cranford *et al.* 2011). Further, in those species with two nearly symmetrical bursae complexes whose anatomy has been studied (*Phocoena phocoena*, *P. dioptrica*, *P. dalli*, *Cephalorhynchus commersonii*), the posterior melon ends abruptly at the nasal plugs with no direct lipid connections to the bursae complexes (Heyning 1989, Amundin and Cranford 1990, Cranford *et al.* 1996, McKenna *et al.* 2012; also note that *C. hectori* has similar posterior melon termination anatomy (Mead 1975), however, the bursae complex has not been well-described for this species). Conversely, genera with two asymmetrical bursae complexes (e.g., most delphinids) tend to produce clicks with a broad frequency bandwidth, bimodal peaks in the frequency spectrum, and a short-duration, oligocyclic waveform, and the posterior melon bifurcates laterally into two branches of which the right branch connects directly to the right bursae complex (Amundin and Cranford 1990, Cranford *et al.* 1996, Cranford and Amundin 2004, McKenna *et al.* 2012). Furthermore, for this click type, an additional *subtype* that exhibits a unique spectral peak banding structure (Soldevilla *et al.* 2008) has been described in some (*Grampus griseus* and *L. obliquidens*: Soldevilla *et al.* 2008; *L. albirostris*: Calderan *et al.* 2013; and *Globicephala macrorhynchus*: Baumann-Pickering *et al.* 2015) but not all delphinid species (Soldevilla *et al.* 2017). Species producing this click subtype tend to have two slightly or moderately asymmetric bursae complexes, and their posterior melon has lateral branches that extend through unique pyramidal lipid basins to connect with both bursae complexes (Cranford *et al.* 1996, McKenna *et al.* 2012, Soldevilla *et al.* 2017).

Considering the relationship between sound production morphology and spectral and temporal structure of echolocation clicks, and that there are fewer species with clear descriptions of sound production morphology than of click characterizations, similarities among described click features may indicate anatomical similarities among related taxa. Therefore, click characteristics may provide indirect evidence of evolutionary relationships. Both *L. australis* and *L. cruciger* produce narrow-band clicks with unimodal high-frequency peaks (narrow-band high-frequency or NBHF) and polycyclic waveforms, similar to those produced by *Cephalorhynchus* species (Table 3; reviewed in Morisaka and Connor 2007; Kyhn *et al.* 2009, 2010; Tougaard and Kyhn 2010). Three of the remaining *Lagenorhynchus* species and one *Lissodelphis* species produce broadband, oligocyclic clicks (*L. obscurus*: Au and Würsig 2004; *L. albirostris*: Rasmussen and Miller 2004; *L. obliquidens*:

Table 3. Summary of acoustic similarities and differences among *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species (as currently named).

Species	Produce whistles?	Type of echolocation click produced	Clicks have spectral banding?	Bursae complex asymmetry	Morphology of the melon and bursae complex
<i>L. acutus</i>	Likely ^{a, b}	Unknown	Possibly ^b	Unknown	Unknown
<i>L. albirostris</i>	Yes ^{c, d}	Broadband ^e	Yes ^f	Slight ^{g, †}	Branched, pyramidal extension, bilateral connection ^g
<i>L. australis</i>	No ^{h, i}	NBHF ⁱ	Unknown*	Unknown	Unknown
<i>L. cruciger</i>	No ^j	NBHF ^{j, k}	Unknown*	Unknown	Unknown
<i>L. obliquidens</i>	Unknown	Broadband ^l	Yes ^m	Slight ^g	Branched, pyramidal extension, bilateral connection ^{g, n}
<i>L. obscurus</i>	Unknown	Broadband ^o	Possibly ^p	Unknown	Unknown
<i>C. commersonii</i>	No ^{1, q}	NBHF ^{r, t, s}	Unknown*	Slight ^{t, u}	Abrupt termination, discontinuous melon and bursae complexes ^{v, w}
<i>C. eutropia</i>	No ^x	NBHF ^x	Unknown*	Unknown	Unknown
<i>C. beavisidii</i>	No ^{y, z}	NBHF ^z	Unknown*	Unknown	Unknown
<i>C. bectori</i>	No ^{aa, bb}	NBHF ^{k, cc}	Unknown*	Unknown	Abrupt termination, discontinuous melon and bursae complexes ^{dd}
<i>L. borealis</i>	No ^{ee, ff}	Broadband ^{ff}	No ^{gg}	Unknown	Branched, pyramidal extension, bilateral connection ^{g, ††}
<i>L. peronii</i>	Unknown	Unknown	Unknown	Unknown	Unknown

*Note that the feature of spectral banding may not be applicable for those species that produce narrow-band high-frequency (NBHF) clicks.

[†]This finding is preliminary since conclusions concerning *L. albirostris* were not based on direct measurements but rather on comparisons between CT scans of *L. albirostris* and *L. obliquidens*.

^{††}This finding is preliminary since the *L. borealis* specimen used for comparisons was a neonate.

^aSteiner 1981; ^bHamran 2014; ^cRendell *et al.* 1999; ^dRasmussen and Miller 2002; ^eRasmussen and Miller 2004; ^fCalderan *et al.* 2013; ^gCranford *et al.* 1996; ^hSchevill and Watkins 1971; ⁱKyhn *et al.* 2010; ^jTougaard and Kyhn 2010; ^kKyhn *et al.* 2009; ^lNakamura and Akamatsu 2004; ^mSoldevilla *et al.* 2008; ⁿMcKenna *et al.* 2012; ^oAu and Würsig 2004; ^pS. Rankin (see note 7 above); ^qDziedzic and De Buffrenil 1989; ^rKamminga and Wiersma 1981; ^sKamminga and Wiersma 1982; ^tCranford and Amundin 2004; ^uCranford *et al.* 2011; ^vAmundin and Cranford 1990; ^wHeyning 1989; ^xGotz *et al.* 2010; ^yWatkins *et al.* 1977; ^zMorisaka *et al.* 2011; ^{aa}Dawson 1991; ^{bb}Dawson and Thorpe 1990; ^{cc}Dawson 1988; ^{dd}Mead 1975; ^{ee}Leatherwood and Walker 1979; ^{ff}Rankin *et al.* 2007; ^{gg}Soldevilla, unpublished data.

Nakamura and Akamatsu 2004; *L. borealis*: Rankin *et al.* 2007), while the clicks of *L. acutus* and *L. peronii* have not been described. As noted previously, *L. obliquidens* and *L. albirostris* are also known to produce the click subtype with spectral-banding; however, as this subtype has only recently been described, further study is needed to determine if it is produced in other *Lagenorhynchus* species as well. A preliminary review of recordings suggests that spectral peak banding may also be found in *L. obscurus*⁷ and *L. acutus* (e.g., see fig. 7b in Hamran 2014) but further work is needed to confirm that this is the case. Click recordings from *L. borealis* do not reveal the presence of spectral peak banding (MSS, unpublished data). Most of the species discussed in this paper have not been studied in terms of their sound-production morphology, therefore it is unknown whether their bursae complexes are symmetrical or how the melon and bursae complexes connect. The sound-production morphology of *L. obliquidens*, *L. albirostris*, and *L. borealis* (newborn) has been investigated. The two *Lagenorhynchus* species have slightly asymmetric bursae complexes and the unique pyramidal basins connecting the melon to both bursae complexes (Cranford *et al.* 1996, McKenna *et al.* 2012). Although the newborn *L. borealis* similarly had melon morphology that included pyramidal basins (Cranford *et al.* 1996), the clicks of *L. borealis* are not known to have spectral peak banding. *Grampus griseus* also shares these same melon features and indeed does produce clicks with spectral banding (Cranford *et al.* 1996, Soldevilla *et al.* 2017), thus highlighting the complex relationship between click structure and sound production morphology.

In summary, the similarities in NBHF click structure among *L. cruciger*, *L. australis*, and the *Cephalorhynchus* species add evidence in support of the morphological and genetic similarities described in previous sections. However, the evolution of NBHF clicking in *Lagenorhynchus*, *Cephalorhynchus*, Kogiidae, and Phocoenidae may represent convergent evolution driven by “acoustic crypsis” to avoid detection by predatory killer whales (*Orcinus orca*; Morisaka and Connor 2007). Furthermore, findings concerning the click subtype with spectral banding and sound production morphology suggest a closer relationship among *L. acutus*, *L. albirostris*, *L. obliquidens*, and *L. obscurus*—similar to the current taxonomy. However, neither the melon morphology of *L. acutus*, *L. australis*, *L. cruciger*, and *L. obscurus*, nor the click structure of *L. acutus*, *L. obscurus* and the *Lissodelphis* species, has been well studied. Focused studies of similarities and differences in sound production and related morphology in all species of the three focal genera are needed and may offer further insights into the evolutionary relationships among the Lissodelphininae (*sensu* LeDuc *et al.* 1999).

The production of whistles among *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* may also provide evidence of evolutionary relationships. The anatomical mechanism for production of odontocete whistles remains unclear. However, phylogenetic reviews indicate that the ability of odontocete species to produce whistles clusters within taxonomic groups

⁷Personal communication from Shannon Rankin, Southwest Fisheries Science Center, NOAA Fisheries, 8901 La Jolla Shores Drive, La Jolla, CA 92037, U.S.A., January 2013.

(Herman and Tavolga 1980, May-Collado *et al.* 2007, Morisaka and Connor 2007), which suggests that whistle production is a derived feature within odontocetes with secondary losses in several taxa (*e.g.*, Morisaka and Connor 2007, May-Collado *et al.* 2007, Morisaka 2012). However, it is also possible that whistle production evolved independently among families that whistle, followed by secondary loss of whistle production in some delphinid taxa (*e.g.*, Podos *et al.* 2002). Within the three focal genera, whistles have not been recorded in any *Cephalorhynchus* species (Table 3; reviewed in Morisaka and Connor 2007, Gotz *et al.* 2010), *L. cruciger* (Tougaard and Kyhn 2010), or *L. australis* (Schevill and Watkins 1971, Kyhn *et al.* 2010). Conversely, whistles are produced by the well-studied *L. albirostris* (Rendell *et al.* 1999, Rasmussen and Miller 2002), and although less well studied, *L. acutus* also appears to produce whistles (Steiner 1981, Hamran 2014). Studies indicating that *L. obliquidens* (Caldwell and Caldwell 1971), *L. obscurus* (Wang *et al.* 1995), and *L. borealis* (Leatherwood and Walker 1979, Rankin *et al.* 2007) produce whistles may represent misidentifications. For example, the *L. obscurus* whistles were recorded with common dolphins (*Delphinus delphis*) present (Yin 1999), while some described *L. borealis* “whistles” were actually misidentified burst-pulse calls (Leatherwood and Walker 1979). Recent studies indicate that these three species do not commonly, if ever, produce whistles (Yin 1999; Rankin *et al.* 2007, 2008; Henderson *et al.* 2011; Vaughn-Hirshorn *et al.* 2012). Following the assumption that production of whistles reflects evolutionary processes, these studies support that *L. cruciger* and *L. australis* are more similar to *Cephalorhynchus* species in that they do not produce whistles; *L. borealis*, *L. obscurus*, and *L. obliquidens* are similar to one another in that they are probably non-whistlers or only whistle infrequently; and *L. albirostris* and *L. acutus* are more distinct from the other species as they retain whistles in their repertoire. More data from *L. acutus*, *L. obliquidens*, *L. obscurus*, and *Lissodelphis* would increase confidence in this interpretation.

Overall, comparisons of sound production and sound production morphology do not provide for a straightforward interpretation of evolutionary relationships within and among *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* (Table 3). The implications of acoustic similarities and differences are unclear. Convergent evolution of acoustic signals due to environmental drivers, including ambient noise and sound propagation conditions of the habitat, communication requirements, prey types, and predator avoidance, can occur such that phylogenetic reconstruction from acoustics is not necessarily straightforward and should be interpreted with caution.

DISCUSSION AND PROPOSED TAXONOMIC REVISIONS

From the preceding review of the available morphological, genetic, biogeographical, and acoustic evidence, it is clear that phylogenetic relationships within and among the genera *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* have been, and remain, problematic. These results parallel those of Perrin *et al.* (2013), who addressed phylogenetic relationships in

another dolphin subfamily, the Delphininae, and concluded “[t]he paraphyletic nature of these genera and the continued inability to resolve relationships (using morphological or molecular data) is a vexing taxonomic problem.” The underlying problem in many of the analyses we reviewed (including some of the same studies discussed in Perrin *et al.* 2013) is likely the same: none of the analyses conducted to date have included all of the genes from all of the species (Tables 1, 2), or had sufficient geographic coverage within species, some of which have enormous distributional ranges, to encompass intraspecific variability. An underlying issue likely common to both subfamilies—a relatively recent and rapid radiation, possibly complicated further by reticulation (hybridization events between recently diverged species, *e.g.*, Morgenthaler *et al.* 2014) or even potential hybrid origin of species (Amaral *et al.* 2014)—adds to the difficulty of teasing apart evolutionary histories.

Although the phylogenetic relationships among all *Lagenorhynchus*, *Cephalorhynchus*, and *Lissodelphis* species have yet to be completely resolved, some of the relationships within the Lissodelphininae (*sensu* LeDuc *et al.* 1999) are well-supported (*e.g.*, in most of the studies reviewed above, *Lissodelphis* was recovered as monophyletic and a sister group of *Cephalorhynchus* and *Lagenorhynchus*) or have some support (*e.g.*, Pichler *et al.* 2001 found *Cephalorhynchus* to be a monophyletic group sharing exclusively two to five diagnostic fixed differences and a shared deletion in control region sequences). Morphological, genetic, and biogeographical data, with some supporting acoustic findings, provide clear and substantial evidence that the current taxonomic classification of the genus *Lagenorhynchus* is not correct. Therefore, we propose that the lack of full generic resolution should not preclude making taxonomic revisions for evolutionary relationships that do have moderate or strong supporting evidence (Table 4).

We have summarized four specific lines of evidence that can be used to support the distinctiveness of the six species currently classified as *Lagenorhynchus* Gray, 1846, and also indicate that division of these species into at least three genera is appropriate. Therefore, where monophyly is clearly not supported, we propose the following taxonomic revisions (that were initially suggested by LeDuc *et al.* 1999) for species formerly considered under *Lagenorhynchus*, and suggest retaining the current taxonomy for *Lissodelphis* and *Cephalorhynchus* unless and until evolutionary relationships among all Lissodelphininae species (*sensu* LeDuc *et al.* 1999) are further clarified:

- Retain the naming of *Lagenorhynchus albirostris* Gray, 1846, the white-beaked dolphin, as this nominal species is the type species for *Lagenorhynchus* Gray, 1846. However, based on the strong genetic, morphological, and biogeographical evidence, as well as evidence from whistle production (Table 4), the remaining five species now assigned to *Lagenorhynchus* do not belong in this genus and are assigned to other genera.
- Resurrect the genus *Leucopleurus* Gray, 1866 for *Delphinus acutus* Gray, 1828, the Atlantic white-sided dolphin. The genetic, morphological, and biogeographical evidence, as well as evidence from whistle production, support separating this species from the other four currently recognized

Lagenorhynchus species (Table 4). This nominal species will become the type species for *Leucopleurus*.

- Resurrect the genus *Sagmatias* Cope, 1866 for the remaining four species. Multiple lines of evidence do not provide consistent support for splitting these species into more than one genus and these four dolphins should be retained in a single genus pending additional analyses that clarify evolutionary relationships with *Cephalorhynchus*. The nominal species *Phocoena australis* Peale, 1849,⁸ Peale's dolphin, becomes the type species for this genus. Also placed in *Sagmatias* are the nominal species *Delphinus cruciger* Quoy and Gaimard, 1824, the hourglass dolphin; *Delphinus obscurus* Gray, 1828, the dusky dolphin; and *Lagenorhynchus obliquidens* Gill, 1865, the Pacific white-sided dolphin.
- Retain the naming and grouping of the four species of *Cephalorhynchus*. As discussed above, missing data, missing taxa, and failure to include a substantial control region indel in analyses conducted to date have hampered attempts to resolve relationships with strong statistical support. Therefore, we recommend retention of species currently assigned to this genus until further evidence can be provided.
- Retain the naming and grouping of the two species of *Lissodelphis*. The nominal species *Lagenorhynchus thicolea* Gray, 1846 is reassigned to *Lissodelphis* Gloger, 1841 as it is a synonym of either *L. peronii* or *L. borealis*.
- Revise the subfamily associations. The subfamily Lissodelphininae Fraser and Purves, 1960 continues to include the genera *Cephalorhynchus*, *Lissodelphis*, and *Sagmatias*. The subfamily associations of *Lagenorhynchus albirostris* and *Leucopleurus acutus* remain *incertae sedis*.

KNOWLEDGE GAPS AND FUTURE RESEARCH

Morphology

No single morphological study has assessed both skull and postcranial measurements from multiple individuals per species from all of *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias*. Using well-established measurements and meristics (e.g., Perrin 1975), collecting both skull and postcranial data, and being aware of specimen sex and maturity are imperative for future work examining internal morphological characteristics. In order to capture the most accurate depiction of intra- and interspecific morphological variation upon which to build a phylogeny, thorough sampling within each species across its natural range is essential given the broad (e.g., *S. obliquidens*) and for some species very disjunct (e.g., *S. obscurus*) ranges. Furthermore, the basic collection and location information for all samples used in analyses should be included in publications.

Although variation in color pattern has been applied as a useful line of evidence to describe differences within some cetacean taxa (e.g.,

⁸This reference is often cited as 1848, however, it was not published until June 1849 (see Bruce *et al.* 2016).

Table 4. Supporting evidence for various phylogenetic hypotheses for the evolutionary relationships among the species of *Lagenorhynchus*, *Lissodelphis*, and *Cephalorhynchus* (as currently named). Genetics studies include those that used mitochondrial DNA (mtDNA) and/or nuclear DNA (nuDNA), with the former separated into those that incorporated data from the mitochondrial control region (w/mtCR) and those that did not (no mtCR). For morphology and genetics studies, species that “group” together form a monophyletic clade; for biogeography and acoustics studies, “group” denotes general similarity. For the genetics studies, only clades with posterior probability values ≥ 0.95 and bootstrap proportions $\geq 70\%$ (when given in the analysis) are considered to be monophyletic. Note that all 12 species are not included in all referenced studies.

	<i>L. albirostris</i> distinct from all	<i>L. acutus</i> distinct from all	<i>L. australis</i> and/or <i>L. cruciger</i> group with <i>Cephalorhynchus</i> *	<i>L. australis</i> , <i>L. cruciger</i> , <i>L. obliquidens</i> , and <i>L. obscurus</i> group with <i>Cephalorhynchus</i> **	<i>Lissodelphininae</i> (<i>sensu</i> LeDuc <i>et al.</i> 1999) group together
Morphology	a, b	a, b	b	b	
Genetics					
mtDNA (no mtCR)	c, d, g, k, l	c, d, e, f, g, k, l		e, f, k	d, e, f, k, l
mtDNA (w/mtCR)	c	c		h	h
nuDNA	k, l	k, l	l		k
mt + nuDNA (no mtCR)	i, j, k, l	i, j, k, l	l	l	i, j, k, l
mt + nuDNA (w/mtCR)	i	i			i
Biogeography					l
Acoustics†					
whistle	o, p	q, r	m - q		
click type			s - z, aa		

*To the exclusion of *L. obliquidens* and *L. obscurus*.

**To the exclusion of both *Lissodelphis* species.

†Most of the acoustics studies referenced here present data on only 1 or 2 of the focal species; only Kyhn *et al.* (2010) and Tougaard and Kyhn (2010) discuss the phylogenetic implications of the acoustic data from *Lissodelphininae* (*sensu* LeDuc *et al.* 1999).

^aMiyazaki and Shikano 1997b, ^bMoreno 2008, ^cCipriano 1997, ^dLeDuc *et al.* 1999, ^eMay-Collado and Agnarsson 2006, ^fAgnarsson and May-Collado 2008, ^gSlater *et al.* 2010, ^hPichler *et al.* 2001, ⁱHarlin-Cognato and Honeycutt 2007, ^jSteele *et al.* 2009, ^kMcGowen 2011, ^lBanguera-Hinestroza *et al.* 2014a, ^mDawson 1991, ⁿSchevill and Watkins 1971, ^oRendell *et al.* 1999, ^pRasmusson and Miller 2002, ^qSteiner 1981, ^rHamran 2014, ^sDawson 1988, ^tEvans *et al.* 1988, ^uGotz *et al.* 2010, ^vMorisaka *et al.* 2011, ^wKyhn *et al.* 2009, ^xTougaard and Kyhn 2010, ^yKyhn *et al.* 2010, ^zAu and Würsig 2004, ^{aa}Nakamura and Akamatsu 2004.

killer whales: Baird and Stacey 1988, Pitman and Ensor 2003, Morin *et al.* 2010, Mäkeläinen *et al.* 2014), color variants have previously led to erroneous taxonomic classifications (*e.g.*, Fraser and Noble 1970, Houck and Jefferson 1999). It is well known that pigmentation patterns of cetaceans can vary individually, geographically, and ontogenetically (Perrin 2018). For *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias* species, we suggest caution when using coloration as a morphological character for phylogenetic analysis as anomalous color patterns and variants have been particularly well documented: *L. acutus* (Weinrich *et al.* 2001), *L. albirostris* (Bertulli *et al.* 2016), *S. obliquidens* (Brownell 1965, Tsutsui *et al.* 2001, Sekiguchi *et al.* 2014), *S. obscurus* (Van Waerebeek 1993a), *C. commersonii* (Iñíguez and Tossenberger 2007, but also see Morgenthaler *et al.* 2014 who considered the individuals in question to be *C. commersonii* x *C. eutropia* hybrids), *L. borealis* (Nishiwaki 1972, Leatherwood *et al.* 1982), and even a possible hybridization between *S. obscurus* and *L. peronii* (Yazdi 2002). Furthermore, it is likely that within a given species not all color variants have yet been described, especially for rarely observed species such as *S. cruciger* (see Van Waerebeek *et al.* 1997b).

Genetics and Biogeography

An appropriate starting point for future studies examining taxonomic relationships of cetaceans, in terms of sample/data collection and analyses, can be found in Taylor *et al.* (2017), who provide guidelines and standards for use of genetic data. Below, we highlight additional considerations applicable especially for investigating relationships among *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias*.

Overall, phylogenetic analyses support the subfamily Lissodelphininae (with the exclusion of *L. acutus* and *L. albirostris*, as described by LeDuc *et al.* 1999), and the early divergence of *L. acutus* and *L. albirostris* in the evolutionary history of the family Delphinidae. However, inconsistencies are evident among phylogenetic studies involving the relationship between the *Cephalorhynchus* species and *S. cruciger* and *S. australis* (Fig. 2, 3). Resolution of these evolutionary relationships is hindered by the insufficiency of available genetic samples, particularly for *S. cruciger* and often for *S. australis* as well. In fact, the only genetic studies that include a complete data set (in terms of marker amplification) for either of these Southern Hemisphere dolphins are those using mitochondrial data only, from either the mtCR or *cyt-b*. The impact on phylogenetic reconstruction of not having such data is unclear but cannot be disregarded. The use of longer sequences and increased character sampling can mitigate the effect of incomplete taxon sampling on phylogenetic accuracy (Rosenberg and Kumar 2001), a strategy to which recent “big data” studies have adhered (*e.g.*, McGowen 2011, Banguera-Hinestroza *et al.* 2014a). However, the specific relationships yet to be resolved in these big data studies involve those taxa with the most sampling gaps (*i.e.*, *S. cruciger* and *S. australis*). It is possible that filling in the missing data within each taxon and additionally increasing

the amount of genetic data across taxa would be the definitive steps needed to increase the statistical support for phylogenetic inferences (e.g., Huelsenbeck 1991, Agnarsson and May-Collado 2008, Hartmann and Vision 2008, Lemmon *et al.* 2009, Xia 2014).

Additionally, future studies should continue to use *both* mitochondrial and nuclear data, and analyses should be conducted on each type of data separately and as a combined data set, because combining data sets has the potential to improve resolution and statistical support for phylogenetic reconstructions (Baker and Gatesy 2002, Rubinoff and Holland 2005). Continued investigation into the utility of additional mitochondrial and nuclear regions for analyses is also warranted as it is possible that the most informative genetic markers to discern some of the finer-scale relationships among *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias* species have yet to be discovered. From the studies cited herein, a total of five mitochondrial and at least 25 nuclear gene regions have been amplified, but well-supported congruence between mitochondrial and nuclear trees has yet to be recovered. Research is also needed to determine the usefulness of diagnostic insertion/deletion events (indels), like those seen in *Cephalorhynchus* species, for taxonomic discrimination. Other rare molecular event synapomorphies, such as the presence of repetitive elements such as SINES (short interspersed nuclear elements) and LINES (long interspersed nuclear elements), have been shown to provide excellent markers for phylogenetic analysis (Bashir *et al.* 2005). For example, Shimamura *et al.* (1997) used such evidence to show that hippopotamuses are the closest living relatives of all cetaceans. Furthermore, taking advantage of next-generation sequencing techniques that are capable of producing large data sets containing thousands of markers, or even whole genomes, is a promising strategy to help gather different types of molecular markers and increase the resolution of complex evolutionary relationships among delphinid taxa. Techniques such as targeted capture (e.g., Bragg *et al.* 2016), amplification of ultraconserved elements (e.g., McCormack *et al.* 2012), and mitogenome sequencing (e.g., Vilstrup *et al.* 2011) have been demonstrated as useful tools to investigate evolutionary relationships among genera and higher order relationships (e.g., placental mammals). Additionally, transcriptome sequencing (e.g., Hittinger *et al.* 2010), although more often used for species-level comparisons, has also demonstrated potential for utility in higher-level phylogenetic comparisons (McCormack *et al.* 2013).

The resolution of past biogeographical patterns could be enhanced by incorporation, and increased sampling, of species in the Southern Hemisphere (particularly *S. cruciger* and *S. australis*) and through incorporation of any fossil evidence as it becomes available. Consistent estimates of dispersal direction among *Sagmatias* species, such as *S. obliquidens* and *S. obscurus* in the Pacific, would also help to further clarify the evolutionary relationships both within this genus and between *Sagmatias* and *Cephalorhynchus* species.

Acoustics

Acoustic evidence based on whistle and click production provides some support for close relationships among *S. australis*, *S. cruciger*, and

Cephalorhynchus species, a finding mirrored by some of the genetic and morphology studies mentioned above (Fig. 2, 3). However, for most of the species within the focal genera there is a need for further descriptions of whistle and click characteristics and sound production morphology (Table 3), including additional acoustic sampling across species' ranges, to improve understanding and bolster the evidence concerning evolutionary relationships among *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias*. Furthermore, work is needed to better understand the relationships of NBHF clicks, broadband, bimodal frequency clicks, and spectral peak banded clicks to sound production morphology for phylogenetic inference. These characteristics have not been well described for most of the species discussed here (Table 3). While acoustic characteristics alone might not constitute a strong enough line of evidence to justify taxonomic changes, acoustics have been a strong line of supportive evidence concerning evolutionary relationships described in other cetacean taxonomic studies (e.g., ecotypes of killer whales: Ford 1991, Barrett-Lennard *et al.* 1996, Foote and Nystuen 2008). As such, there is a need for future studies to fill in acoustic data gaps, especially those that may be helpful in discerning complex systematic relationships.

Directions for Future Sampling and Research

Future research is bound to encounter challenges with regard to funding, time, and/or sample availability/accessibility. A cost-effective strategy for work focused on *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias* could be to design interdisciplinary, collaborative proposals for projects that maximize the amount of information gained from a given specimen. For example, work focused on obtaining measurements from skulls and skeletons could also include the collection of teeth or bone for collaborative genetic analyses. Additional analyses of internal sound production morphology through CT scanning or MRI, in conjunction with acoustic recordings, are needed to better characterize differences and similarities between species and species groups. Communication with the stranding response community is also important to make sure that appropriate methods are used to collect internal and external morphological data as well as to sample soft tissue (e.g., skin, muscle) for genetic studies. Research expeditions (e.g., sponsored by tourism, academic institutions, or government agencies) focused on areas in the Southern Ocean and surrounding Antarctica could enhance their primary research objectives by adding concurrent opportunistic sampling (e.g., genetic biopsy, acoustic recording, photography) of small delphinids such as *S. cruciger* and *L. peronii*, for which dedicated research cruises to that region may not be feasible or affordable. Furthermore, it is imperative that museums, universities, and other biorepositories communicate openly and regularly with scientists and make known what is available in terms of acoustic recordings, genetic and morphological specimens, and even photographs and CT scans both to help determine where future work is needed and prevent duplication of effort.

CONCLUSIONS

While the field of molecular genetics has evolved rapidly in recent years, allowing for extensive data sets to be easily (relatively speaking) compiled and made accessible to phylogeneticists, there remains the issue of truly representative sampling within species and across species' ranges. More data, in terms of samples and genetic information, are needed to resolve and quantify remaining uncertainties and achieve finer-scale resolution of the taxonomic relationships among *Cephalorhynchus*, *Lagenorhynchus*, *Leucopleurus*, *Lissodelphis*, and *Sagmatias*. The same can certainly be argued for studies incorporating morphological, acoustic, and behavioral data.

Furthermore, while data from morphology, genetics, biogeography, and acoustics support taxonomic changes for species such as *L. acutus* and *L. albirostris*, and have corroborated the findings of LeDuc *et al.* (1999), there is still a lack of support from multiple lines of evidence for making definitive statements about the phylogenetic relationships within the Lissodelphininae (*sensu* LeDuc *et al.* 1999). If improved analyses indicate that the pairwise differences between *cruciger/australis* and *obscurus/obliquidens* are indeed strong enough to warrant genus-level recognition, a new genus name will be required for the latter pair as none of the synonyms for *obscurus* or *obliquidens* are available. However, current uncertainties should not prevent taxonomic reclassifications for the systematic relationships that are currently well supported by multiple independent lines of evidence. Making taxonomic revisions now will help to plan future research, allocate funding and effort, and structure data sets and analyses to address the phylogenetic, systematic, and taxonomic questions concerning these rapidly evolved species.

TAXONOMIC TREATMENT AND SPECIES DESCRIPTIONS

Unique publications written by the same author within a single year are differentiated in the synonymies by the addition of *a*, *b*, or *c* after the authority name and year and before the corresponding page, plate, or figure number (*e.g.*, *Lagenorhynchus* Gray, 1846*a*:84). This was done to be able to correctly identify corresponding citations within the Literature Cited. Outside of the synonymies and appendices we refrained from using this notation and instead used the traditional notation for naming authorities (*e.g.*, *Lagenorhynchus* Gray, 1846); therefore, to identify the correct citation for a given name readers must refer back to the relevant synonymy or appendix. Furthermore, we differentiated between a literature citation, *e.g.*, Gray 1846 or Gray (1846) and a naming authorship, *e.g.*, Gray, 1846 or (Gray, 1846) by the absence or presence, respectively, of a comma between the author name and year. The synonymies were formatted based on the guidelines of Gardner and Hayssen (2004). More information for the species presented here can be found in Appendix 1: Nomenclatural Notes, which provides additional information for each species listed in the synonymies below; and Appendix 2: Misidentifications, which includes information regarding

misidentifications associated with *Lagenorhynchus* synonymies and the genus name *Lagenorhynchus* appearing in the synonymies of other genera (e.g., *Cephalorhynchus*).

Order Cetartiodactyla Montgelard, Catzefils and Douzery, 1997
Cetacea (Brisson, 1762)
Family Delphinidae Gray, 1821
Subfamily *incertae sedis*
Retention of genus *Lagenorhynchus* Gray, 1846

SYNONYMY

Delphinus Linnaeus, 1758:77. Type species *Delphinus delphis* Linnaeus, 1758 by absolute tautonymy.
Lagenorhynchus Gray, 1846a:84. Type species *Lagenorhynchus albirostris* Gray, 1846 by monotypy.

TYPE SPECIES

Lagenorhynchus albirostris Gray, 1846

INCLUDED SPECIES

Lagenorhynchus albirostris Gray, 1846

HOLOTYPE

According to Hershkovitz (1966), the holotype of *L. albirostris* Gray, 1846 consists of a skeleton and figure of the dolphin in the British Museum (Natural History), London, catalog no. 916a-48.7.12.12. The online catalog of the British Museum (accessed 23 June 2017) lists the specimen as no. 1848.7.12.12.

TYPE LOCALITY

The holotype was collected from Great Yarmouth, England by T. Brightwell. No type locality was specified by Gray (1846a), but it was described as “North Sea, coast of Norfolk” (England) by Gray (1846b) and specified as “Yarmouth” by Gray (1850a).

ETYMOLOGY

The generic name *Lagenorhynchus* is derived from the Greek *lagenos* for “bottle” or “flask” and *rhynchus* for “beak” or “snout.”

DIAGNOSIS

Occurring across the North Atlantic, *L. albirostris* largely overlaps in distribution with *L. acutus* but can be differentiated based on its light gray or white beak, the presence of a grayish-white saddle behind the dorsal fin, the lack of a yellow/tan blaze along the flank, and a gradually tapering tail stock. Compared to *L. acutus*, *L. albirostris* has a shorter

(<240 mm) and wider at the base rostrum (>125 mm) and fewer, but larger, teeth (see *Meristics and osteology* below for tooth count; Reeves *et al.* 1999a, Galatius and Kinze 2016). Additionally, *L. albirostris* can be distinguished from all *Sagmatias* and *Leucopleurus* species based on cranial characteristics, including having the largest condylobasal length, width of external nares, braincase length, and preorbital width, and by having a greater vertebral count (Miyazaki and Shikano 1997b).

Numerous molecular phylogenies, using nuclear and/or mitochondrial markers, have shown that *L. albirostris* is differentiated from *Leucopleurus acutus* and all *Sagmatias*, *Cephalorhynchus*, and *Lissodelphis* species with high statistical support based on phylogenetic bootstrap and Bayesian posterior probability (PP) values (Fig. 2, 3; Table 4). These studies reveal that *L. albirostris* has no close genetic affinity to any other species in these genera, supporting the monotypic status of this genus.

DISTRIBUTION

Lagenorhynchus albirostris inhabits cold-temperate and arctic waters across the North Atlantic generally from 40°N to 80°N (Fig. 1A). The species has been documented to be more numerous in the eastern North Atlantic (Northridge *et al.* 1997). In the western North Atlantic, it typically is found as far south as Cape Cod, in the Gulf of Maine and north into the Gulf of St. Lawrence, on the Labrador Shelf, and along the southwest coast of Greenland (Alling and Whitehead 1987; Northridge *et al.* 1997; Reeves *et al.* 1999a, 2002; Hansen and Heide-Jørgensen 2013; Galatius and Kinze 2016; Kinze 2018; NAMMCO 2018). It ranges across the North Atlantic along Greenland's east coast and throughout Icelandic waters, along the west coast of Svalbard, and throughout the Barents Sea (Northridge *et al.* 1997; Reeves *et al.* 1999a, 2002; Fall and Skern-Mauritzen 2014; Jefferson *et al.* 2015; Galatius and Kinze 2016; Kinze 2018; NAMMCO 2018). In the eastern North Atlantic, *L. albirostris* occurs along the Norwegian coast, south throughout the Norwegian and North Seas, the surrounding waters of the United Kingdom and Ireland, and along the European coastline from Denmark to southwestern France (Kinze *et al.* 1997; Northridge *et al.* 1997; Reeves *et al.* 1999a, 2002; Jefferson *et al.* 2015; Galatius and Kinze 2016; Kinze 2018).

Marginal localities—Stranded individuals have been documented along the U.S. east coast as far south as New Jersey (38°N) and North Carolina (34°N; Thayer *et al.* 2018), and sightings of live animals have been documented on two occasions in Canadian waters of the western Davis Strait along southeastern Baffin Island (Reinhart *et al.* 2014). A few records have been reported from the southern Bay of Biscay (Castells and Mayo 1992), as well as numerous sightings of *L. albirostris* reported in recent years off the coast of Portugal between 39°N and 40°N (Vingada and Eira 2018), and at least two stranding events along the northern coast of Spain in Cantabria (García-Castrillo Riesgo 1987,

L. Laria⁹). There is an unconfirmed report from the Strait of Gibraltar in 1987 (Hashmi and Adloff 1991), but there have been no further reported sightings of white-beaked dolphins in that area since then.¹⁰

Retention of *Lagenorhynchus albirostris* Gray, 1846

COMMON NAME

White-beaked dolphin

SYNONYMY

Delphinus Tursio: Brightwell, 1846:21, Plate 2. Not *Delphinus tursio* Fabricius, 1780. Unavailable name, misidentification.

Lagenorhynchus albirostris: Gray, 1846a:84. No type locality specified but is described as “North Sea, coast of Norfolk” (England) by Gray (1846b) and specified as “Yarmouth” (Gray 1850a). First use of current name combination.

Delphinus albirostris: Gray, 1846b:35, Plates 10 and 11. Name combination.

Delphinus pseudotursio Reichenbach, 1846:Plate 24, Figure 76. No type locality specified.

Delphinus Ibsenii Eschricht, 1846:297. No type locality specified but is stated as “N. Atlantic: Denmark” in Hershkovitz (1966) and “Agger Tange, West coast of Jutland, Denmark” in Galatius and Kinze (2016).

Delphinus (Lagenorhynchus) albirostris: Van Bénédén, 1860:28. Name combination.

HOLOTYPE

Same as above for “*Lagenorhynchus*”

TYPE LOCALITY

Same as above for “*Lagenorhynchus*”

ETYMOLOGY

The species name *albirostris* is derived from the Latin *albus* meaning “white” and *rostrum* meaning “beak” or “snout.”

DIAGNOSIS

Same as above for “*Lagenorhynchus*”

⁹Personal communication from Luís Laria, Coordinadora para el Estudio y Protección de las Especies Marinas-CEPESMA, Muelle 3, E-33700-Luarca, Asturias, Spain, 9 November 2018.

¹⁰Personal communication from Giuseppe Notarbartolo di Sciarra, Tethys Research Institute, Via Benedetto Marcello 43, 20124, Milano, Italy, 17 April 2018.

DISTRIBUTION

Same as above for "*Lagenorhynchus*"

DESCRIPTION

Coloration—The color pattern of *L. albirostris* can be variable between individuals and across ages (Mercer 1973, Camphuysen 1991, Bertulli *et al.* 2016), and the general color pattern is briefly described here (also see Reeves *et al.* 1999a, 2002). The rostrum of *L. albirostris* is often light gray or white in color and the dorsal fin is dark. The anterior dorsal surface is dark-gray and there is a grayish-white saddle behind the dorsal fin. The belly is typically white and the flippers are dark-gray. Laterally, dark patches are interrupted by light-gray and white blazes with the anterior portion of the peduncle often appearing light-gray to white.

Body form—*Lagenorhynchus albirostris* has an overall robust body shape with a relatively short rostrum that is distinctly offset from the melon. The dorsal fin is mid-body, tall, falcate, and proportionately large (up to 15% of the body length; Reeves *et al.* 1999a). The tail stock gradually tapers toward the fluke. Sexual dimorphism is evident for this species with males having a longer total body length than females (Dong *et al.* 1996, Reeves *et al.* 1999a, Galatius *et al.* 2013).

Meristics and osteology—*Lagenorhynchus albirostris* has 21–28 upper and 24–28 lower teeth ($n = 14$; Table S1; van Bree and Nijsen 1964) and a total vertebral count of between 85–91 ($n = 12$; Table S1; van Bree and Nijsen 1964, Miyazaki and Shikano 1997b, Buchholtz and Schur 2004).¹¹ Based on animals from the eastern North Sea, condylobasal length for adult females was 415–452 mm, mean 444 mm ($n = 16$), and for adult males 435–464 mm, mean 451 mm ($n = 12$; Galatius and Kinze 2016). Total body length of animals from the North Sea was 252–290 cm for males ($n = 7$) and 242–265 cm for females ($n = 17$; Galatius *et al.* 2013). Animals off Newfoundland were estimated to reach physical maturity at an average body length of 261 cm for females ($n = 4$) and 281 cm for males ($n = 4$; Dong *et al.* 1996). The largest measured specimen was a male stranded in the British Isles (310 cm; Fraser 1974). Additional morphological and osteological characters are described in Galatius and Kinze (2016).

Variation (geographic or other)—Genetic variation, assessed using both nuclear and mitochondrial DNA data, supports the presence of two differentiated populations of *L. albirostris* in the British Isles/North Sea and Norway/Barents Sea (Banguera-Hinestroza *et al.* 2010). Hill Mikkelsen and Lund (1994) found significant morphological differentiation in skull measurements between *L. albirostris* from the eastern and western North

¹¹Tooth counts include teeth embedded within the jaw, teeth that are completely detached from the jaw, and/or dental alveoli when teeth are missing. It is unknown whether all cited authors included the presence of nonerupted teeth hidden in the gum. Vertebral counts from incomplete skeletons are included and therefore the low end as given represents a minimum.

Atlantic, suggesting the presence of two morphological variants in these waters. An apparent switch in habitat use in the 1970s between *L. albirostris* and *L. acutus* has made *L. albirostris* more common off the continental shelf in U.S. waters of the western North Atlantic (Kenny *et al.* 1996, Palka *et al.* 1997). However, in the eastern North Atlantic, they are associated more often with shelf waters (Northridge *et al.* 1997). Seasonal variation in occurrence has been documented in the western North Atlantic off Labrador where individuals are typically observed after (or as) the ice recedes in June and their abundance increases in summer months (Lien *et al.* 2001). In the Davis Strait, occurrence increases in the spring and summer and they are believed to move southward during winter months (Leatherwood *et al.* 1976). In the eastern North Atlantic from April to June, *L. albirostris* were found to aggregate consistently, over 15 yr of surveys, off the northeast coast of England and in northern Scottish waters (Northridge *et al.* 1997).

Order Cetartiodactyla Montgelard, Catzefils and Douzery, 1997
 Cetacea (Brisson, 1762)
 Family Delphinidae Gray, 1821
 Subfamily *incertae sedis*
 Resurrection of genus *Leucopleurus* Gray, 1866

SYNONYMY

Delphinus Linnaeus, 1758:77. Type species *Delphinus delphis* Linnaeus, 1758 by absolute tautonymy.

*Phocaena*¹² Gray, 1828:2. Type species *Delphinus phocaena* Linnaeus, 1758 [= *Phocaena phocoena* (Linnaeus, 1758)], by monotypy. Considered a subgenus of *Delphinus* Linnaeus, 1758.

Lagenorhynchus Gray, 1846a:84. Type species *Lagenorhynchus albirostris* Gray, 1846 by monotypy.

Electra Gray, 1866a:268. Type species *Lagenorhynchus electra* Gray, 1846 [= *Peponocephala electra* (Gray, 1846)], by absolute tautonymy. Considered a subgenus of *Lagenorhynchus* Gray, 1846. Preoccupied by *Electra* Lamouroux, 1816, a genus of Bryozoa (Hershkovitz 1966). Note that the authority for *Electra* is incorrectly cited as "*Electra* Gray, 1868" in Mead and Brownell (2005:731).

Leucopleurus Gray, 1866b:216. Type species *Delphinus leucopleurus* Rasch, 1843 [= *Lagenorhynchus acutus* (Gray, 1828)], by monotypy. Considered a subgenus of *Lagenorhynchus* Gray, 1846.

Leicopleurus Tomilin, 1957:592. Incorrect subsequent spelling of *Leucopleurus* Gray, 1866.

TYPE SPECIES

Delphinus leucopleurus Rasch, 1843

¹²Throughout the literature there is inconsistent usage of *Phocaena*, *Phocæna*, *Phocoena*, and *Phocæna* and it is likely that many authors misused the "ae" and "oe" diphthong when spelling this genus name.

INCLUDED SPECIES

Leucopleurus acutus (Gray, 1828)

HOLOTYPE

According to Wiig and Bachmann (2013), the syntype of *Delphinus leucopleurus* Rasch, 1843 exists as “NHMO 2645, skeleton with skull” at the Natural History Museum, University of Oslo, Norway.

TYPE LOCALITY

According to Wiig and Bachmann (2013), the syntype was “collected by fishermen at Drøbak, Norway, 1842.”

ETYMOLOGY

The genus name *Leucopleurus* is derived from Greek where *leukos* means “white” and *pleura* means “the side.”

DIAGNOSIS

Leucopleurus acutus partially overlaps in distribution with *L. albirostris* across the North Atlantic and can be differentiated based on the presence of a sharply defined color pattern, in part consisting of a dark gray to black upper jaw and entire dorsal surface, a white lateral patch starting below the dorsal fin and extending posteriorly, a white belly and lower jaw, black flippers, and a yellow or tan blaze along the flank. From a lateral view, the tail stock abruptly tapers prior to the flukes. Compared to *L. albirostris*, *L. acutus* has a longer and narrower skull (Reeves *et al.* 1999b). Additionally, *L. acutus* can be distinguished from all *Sagmatias* species based on having the largest lachrymal length and greatest preorbital width (Miyazaki and Shikano 1997b).

Molecular evidence based on both nuclear and mitochondrial DNA data supports that *L. acutus* is differentiated from *Lagenorhynchus albirostris* and all species of *Sagmatias*, *Cephalorhynchus*, and *Lissodelphis* with high statistical support based on phylogenetic bootstrap and PP values (Fig. 2, 3; Table 4). These studies reveal that *L. acutus* has no close genetic affinity to any other species, supporting the monotypic status of this genus.

DISTRIBUTION

Leucopleurus acutus is found in cold temperate, oceanic waters across the North Atlantic, on the continental shelf and slope, and in deeper oceanic waters (Fig. 1A). It is thought to be more numerous in the western than the eastern North Atlantic (Northridge *et al.* 1997). In the western North Atlantic, *L. acutus* is typically found north of Cape Cod (40°N), into the Gulf of Maine and the Gulf of St. Lawrence, and to the Davis Strait (Testaverde and Mead 1980; Selzer and Payne 1988; Hill Mikkelsen and Lund 1994; Kenny *et al.* 1996; Northridge *et al.* 1997; Palka *et al.* 1997; Reeves *et al.* 1999b, 2002; Jefferson *et al.* 2015; Hayes *et al.* 2016;

Cipriano 2018). Ranging across the North Atlantic, it occurs north along southeastern Greenland, in southern Icelandic waters, along southern Svalbard (Reeves *et al.* 1999b, 2002; Jefferson *et al.* 2015; Cipriano 2018) and in oceanic waters over the Mid-Atlantic Ridge (Doksæter *et al.* 2008). In the eastern North Atlantic, the species occurs along the Norwegian coast, south throughout the Norwegian and North Seas, the surrounding waters of the United Kingdom and Ireland, and along the European coastline from Denmark to northwestern France (Hill Mikkelson and Lund 1994; Kinze *et al.* 1997; Northridge *et al.* 1997; Reeves *et al.* 1999b, 2002; Hamran 2014; Jefferson *et al.* 2015; Cipriano 2018).

Marginal localities—There are a few reported strandings and bycatches as far south in the western North Atlantic as North Carolina (35°N; Palka *et al.* 1997) and South Carolina (33°N; Powell *et al.* 2012), and in the eastern North Atlantic in Spain (between 42°N–44°N; López *et al.* 2002, L. Laria,¹³ A. López¹⁴). In 2011, two sightings of *L. acutus* were reported off the coast of Portugal between 38°N and 40°N (Vingada and Eira 2018). There is an unconfirmed report from the Strait of Gibraltar in 1990 (Hashmi and Adloff 1991), but there have been no further reported sightings of *L. acutus* in that area since then.¹⁵

Redescription of *Leucopleurus acutus* (Gray, 1828)

COMMON NAME

Atlantic white-sided dolphin

SYNONYMY

Delphinus (*Grampus*) *acutus* Gray, 1828:2. No type locality is specified.

Phocaena acutus: Gray in Brookes and Robins, 1828:39. Name combination.

Delphinus Eschrichtii Schlegel, 1841:23, Plates 1 and 2 Figure 4, Plate 4 Figure 5. Type locality is “Fär-Inseln” (Faroe Islands).

Delphinus leucopleurus Rasch, 1843:100, Plates 2 and 3. No type locality specified but is stated as the “Gulf of Christiania” (Norway; Hershkovitz 1966).

Lagenorhynchus leucopleurus: Gray, 1846b:34, Plate 6 Figures 3–5, Plate 12, Plate 26 Figure 3. Name combination.

Lagenorhynchus acutus: Gray, 1846b:36. Name combination.

Electra acuta: Gray, 1868b:7. Name combination.

Leucopleurus arcticus Gray, 1868b:7, Plate 6 Figures 3–5, Plate 12, Plate 26 Figure 3. Type locality is “North Sea.”

Lagenorhynchus perspicillatus Cope, 1876:136, Plate 4. Type locality is “near Portland, Maine” U.S.A.

Lagenorhynchus gubernator Cope, 1876:138. Type locality is “near the same locality as the last” (near Portland, Maine, U.S.A.).

¹³See note 9 above.

¹⁴Personal communication from Alfredo López, Coordinadora para o Estudo dos Mamíferos Mariños-CEMMA, Ap 15, E-36380 Gondomar, Galiza, Spain, 9 November 2018.

¹⁵See note 10 above.

[*Lagenorhynchus*]. *bombifrons* Cope, 1876:138. Nomen nudum.
[*Lagenorhynchus*]. *acutus*: Flower, 1884:489, Figure 8. Name combination.
Leucopleurus arcticus Tomilin, 1957:592. Incorrect subsequent spelling.
Leucopleurus acutus: LeDuc *et al.*, 1999:639, Figure 2. First use of current name combination.
Delphinus leucoplaurus Wiig and Bachmann, 2013:595. Incorrect subsequent spelling.

HOLOTYPE

According to Flower (1884), the holotype of *Delphinus (Grampus) acutus* Gray, 1828 exists as a skull that was originally at the museum of Joshua Brookes and sold to the Leiden Museum of Natural History (Naturalis Biodiversity Center), Netherlands. According to Broekema (1983), the holotype of “*Grampus acutus* Gray, 1828. Skull. Brookes, 1828” is at the Rijksmuseum van Natuurlijke Historie, Leiden as specimen 18281.

TYPE LOCALITY

According to Hershkovitz (1966), the type locality is “[u]nknown; determined as the Faeroe Islands, North Sea, on the basis of the provenance of the subjective synonym *eschrichtii* Schlegel, by Gray... [1846b].”

ETYMOLOGY

The species name *acutus* is derived from Latin and means “sharp” or “pointed.”

DIAGNOSIS

See above for “*Leucopleurus*.”

DISTRIBUTION

See above for “*Leucopleurus*.”

DESCRIPTION

Coloration—*Leucopleurus acutus* has a distinct and sharply defined color pattern consisting of a dark gray or black dorsal surface and dorsal fin, gray along the sides interrupted by a white patch starting under the dorsal fin, continuing posteriorly, and extending into a narrow yellow/tan blaze along the flank towards the flukes. The flippers and flukes are black/dark gray and the lower jaw and belly are white. The eye is ringed in black with a thin black stripe extending to the upper jaw. Aberrantly patterned dolphins have been recorded stranded in both the eastern and western North Atlantic (Jefferson *et al.* 2015, A. Reid¹⁶).

¹⁶Personal communication from Andrew Reid, Marine Animal Response Society, 1747 Summer Street, Halifax, Nova Scotia B3H 3A6, Canada, 8 April 2018.

Body form—*Leucopleurus acutus* has a robust body shape and short rostrum (≤ 5 cm) that is not distinctly offset from the melon (Reeves *et al.* 1999b). The dorsal fin is mid-body, tall, and falcate. The tail stock is keeled, with adult males having a higher and more abruptly narrowed caudal peduncle compared to females (Reeves *et al.* 1999b, Jefferson *et al.* 2015). Sexual dimorphism is evident for this species with males having a greater total body length than females (Sergeant *et al.* 1980).

Meristics and osteology—*Leucopleurus acutus* has 31–41 upper and 30–41 lower teeth ($n = 24$; Table S1) and a total vertebral count between 65–83 ($n = 31$; Miyazaki and Shikano 1997b, Buchholtz *et al.* 2005).¹⁷ Skull measurements from 10 specimens had condylobasal lengths of 399–426 mm, mean 412.5 mm (Miyazaki and Shikano 1997b). The greatest total body length measured from 121 animals stranded in the western North Atlantic was 243 cm for adult females and 267 cm for adult males (Sergeant *et al.* 1980), and from 19 animals stranded in Ireland (eastern North Atlantic) it was 241 cm for females and 274 cm for males (Rogan *et al.* 1997). Females in the western North Atlantic were estimated to reach physical maturity at 201–222 cm in length ($n = 36$; Sergeant *et al.* 1980), and males in the eastern North Atlantic at around 215–230 cm ($n = 25$; Addink *et al.* 1997).

Variation (geographic or other)—Analysis of mitochondrial DNA data revealed significant genetic variation between samples of *L. acutus* in the far northeastern Atlantic (Shetland Isles and East Scotland) and those collected from across the North Atlantic (Banguera-Hinestroza *et al.* 2014b). Furthermore, since an apparent switch in habitat use in the 1970s between *L. albirostris* and *L. acutus* in the western North Atlantic, *L. acutus* has become more common in coastal and offshore waters on the continental shelf (Sergeant *et al.* 1980, Kenny *et al.* 1996, Palka *et al.* 1997). However, in the eastern North Atlantic, this species is more often associated with oceanic waters (Northridge *et al.* 1997). There is also evidence for seasonal variation in *L. acutus* distribution and strandings in the western North Atlantic, where animals are generally centered over Georges Bank and in the Great South Channel throughout the year but with increases in sighting rates within the Gulf of Maine in summer and fall (Northridge *et al.* 1997, Palka *et al.* 1997). Between 1973 and 1999, there was an increase in stranding events between December and February along the Gulf of Maine coast (Amaral 2005). In the eastern North Atlantic, sightings throughout the North Sea decrease substantially from December to April (Northridge *et al.* 1997).

¹⁷See note 11 above.

Order Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997
 Cetacea (Brisson, 1762)
 Family Delphinidae Gray, 1821
 Subfamily Lissodelphininae Fraser and Purves, 1960
 Resurrection of genus *Sagmatias* Cope, 1866

SYNONYMY

- Delphinus* Linnaeus, 1758:77. Type species *Delphinus delphis* Linnaeus, 1758, by absolute tautonymy.
- Phocoena*¹⁸ G. Cuvier, 1817:279. Type species *Delphinus phocoena* Linnaeus, 1758 [= *Phocoena phocoena* (Linnaeus, 1758)], by monotypy.
- Phocoena*¹⁹ Gray, 1828:2. Type species *Delphinus phocoena* Linnaeus, 1758 [= *Phocoena phocoena* (Linnaeus, 1758)], by monotypy. Considered a subgenus of *Delphinus* Linnaeus, 1758.
- Tursio* Wagler,²⁰ 1830:34. Type species *Delphinus peronii* G. Cuvier, 1823 (= *Delphinus peronii* Lacépède, 1804), by monotypy. Preoccupied by *Tursio* Fleming, 1822 (= *Physeter* Linnaeus, 1758).
- Lissodelphis* Gloger, 1841:169. Type species *Delphinus peronii* Lacépède, 1804 [= *Lissodelphis peronii* (Lacépède, 1804)], by monotypy.
- Lagenorhynchus* Gray, 1846a:84. Type species *Lagenorhynchus albirostris* Gray, 1846, by monotypy.
- Cephalorhynchus* Gray, 1846b:36. Type species *Delphinus cephalorhynchus* F. Cuvier, 1836, by absolute tautonymy. Considered a subgenus of *Delphinus* Linnaeus, 1758.
- Clymene* Gray, 1864:237. Type species *Delphinus euphrosyne* Gray, 1846 [= *Stenella coeruleoalba* (Meyen, 1833)], by monotypy. Considered a subgenus of *Delphinus* Linnaeus, 1758. Preoccupied by *Clymene* Lamarck, 1818 and Savigny, 1822, a polychaete (Hershkovitz 1966).
- Sagmatias* Cope, 1866:294. Type species *Sagmatias amblodon* Cope, 1866 [= *Lagenorhynchus australis* (Peale, 1849)], by monotypy.
- Electra* Gray, 1866a:268. Type species *Lagenorhynchus electra* Gray, 1846 [= *Peponocephala electra* (Gray, 1846)], by absolute tautonymy. Preoccupied by *Electra* Lamouroux, 1816, a genus of Byrozoa (Hershkovitz 1966). Note that the authority for *Electra* is incorrectly cited as “*Electra* Gray, 1868” in Mead and Brownell (2005:731).
- Clymenia* Gray, 1868b:6. Type species *Delphinus euphrosyne* Gray, 1846 [= *Stenella coeruleoalba* (Meyen, 1833)], by monotypy. Unjustified emendation of *Clymene* Gray, 1864; preoccupied by *Clymenia* Savi, 1817, a genus of ‘vermes’, Münster, 1834, a mollusk, and Örsted,

¹⁸See note 12 above.

¹⁹See note 12 above.

²⁰Another authority for *Tursio* is Gray, 1843:xxiii, 105. Type species *Tursiops truncatus* Montagu, 1821, by monotypy. It is unclear whether Wagler, 1830 or Gray, 1843 is the appropriate authority for *Tursio* (as applied to *Tursio chiloensis* Philippi, 1900 [= *Sagmatias australis* (Peale, 1849)], *Tursio obscurus* Gray, 1866 [= *Sagmatias cruciger* (Quoy and Gaimard, 1824)], and *Tursio? Panope* Philippi, 1895 [= *Sagmatias obscurus* (Gray, 1828)]). In the synonymy of *Sagmatias* we choose Wagler, 1830 because it precedes Gray, 1843.

1844, a worm (HersHKovitz 1966). Note that Flower (1884:499) states the “type of this group is Gray’s *D. longirostris* (‘Spicilegia,’ p. 1, 1828),” however, it is unclear if Flower is referring specifically to the genus *Clymenia* or to a distinct form (type “D”) of *Clymenia*.

Prodelphinus Gervais in Van Bénéden and Gervais, 1880:604. Type species *Delphinus euphrosyne* Gray, 1846 [= *Stenella coeruleoalba* (Meyen, 1833)], by monotypy. New name for *Clymenia* Gray, 1868 “pour plus de régularité dans la synonymie” [for more regularity in synonymy].

*Phocaena*²¹ Kellogg, 1928:33. This is a list of genus names and there is no indication of what the type species may be.

TYPE SPECIES

Sagmatias amblodon Cope, 1866

INCLUDED SPECIES

Sagmatias australis (Peale, 1849)

Sagmatias cruciger (Quoy and Gaimard, 1824)

Sagmatias obliquidens (Gill, 1865)

Sagmatias obscurus (Gray, 1828)

HOLOTYPE

The holotype of *Sagmatias amblodon* Cope, 1866 is a skull located at the Smithsonian Institution’s National Museum of Natural History, Washington, D.C. (USNM 3887; Fisher and Ludwig 2016). See Holotype and Type Locality for *Sagmatias australis* for more information.

TYPE LOCALITY

The specific type locality of *Sagmatias amblodon* is unknown and the specimen was believed to have been caught at sea, collected “on unknown date by the ship *Vincennes* of the U.S. Exploring Expedition. Original number [MC:2]” (Cope 1866, Fisher and Ludwig 2016). The specimen was likely collected somewhere between Cape Horn, Chile, and Lima, Peru, or in the waters of Australia or New Zealand per the account of the naturalist, Dr. Charles Pickering, aboard the *Vincennes* (Cope 1866). However, based on the restricted range of this species it is very unlikely that it was collected outside of South American waters (see *S. australis* *Distribution* below). In fact, based on the survey track line of the U.S. Exploring Expedition (see Wilkes 1845), there are only a couple of places where the specimen could have been collected in southern South America.

ETYMOLOGY

Cope (1866) does not provide an explanation for the derivation of *Sagmatias* and it is not from a common Greek or Latin root.

²¹See note 12 above.

DIAGNOSIS

There is no overlap in geographical distribution of *Sagmatias* with either *Lagenorhynchus* or *Leucopleurus*. Furthermore, all *Sagmatias* species can be distinguished from *Lagenorhynchus* and *Leucopleurus* based on cranial characteristics including tooth count, lachrymal length, preorbital width, condylobasal length, length of external nares, brain-case length, and vertebral count (Miyazaki and Shikano 1997b).

Molecular data from both nuclear and mitochondrial DNA markers support the differentiation of *Sagmatias* from *Leucopleurus* and *Lagenorhynchus*, as well as from *Lissodelphis* and *Cephalorhynchus* species (Fig. 2, 3). In these phylogenies, a close sister-species relationship is often recovered between *S. australis* and *S. cruciger* and between *S. obliquidens* and *S. obscurus* (Fig. 2, 3; LeDuc *et al.* 1999, Pichler *et al.* 2001, Harlin-Cognato and Honeycutt 2006, May-Collado and Agnarsson 2006, Agnarsson and May-Collado 2008, Slater *et al.* 2010, McGowen 2011, Banguera-Hinestroza *et al.* 2014a).

DISTRIBUTION

Generally, *Sagmatias* species are distributed in oceanic waters of the North Pacific, coastal waters throughout the Southern Hemisphere, and oceanic waters of the Southern Ocean (Fig. 1A). *Sagmatias obliquidens* inhabits the North Pacific from Japan to the Kuril Islands in the west, along the southern Aleutian Islands and throughout the Gulf of Alaska, and along the U.S. coast to Baja California, Mexico in the east. *Sagmatias australis* is found along the southern coast of South America. *Sagmatias obscurus* occurs in much of the Southern Hemisphere, including coastal waters of southeastern Australia, New Zealand, Chile, Peru, and Argentina, various oceanic islands of the South Atlantic and Indian Oceans, and off southwestern South Africa. *Sagmatias cruciger* is distributed throughout oceanic waters of the Southern Ocean (see below for more detailed species-specific distributions).

Redescription of *Sagmatias australis* (Peale, 1849)

COMMON NAME

Peale's dolphin

SYNONYMY

Phocaena australis Peale, 1849:33. Type locality is "the South Atlantic Ocean, off the coast of Patagonia."

Delphinus obscurus (in part): Cassin, 1858:27, Plate 5 Figure 1. Name combination.

Sagmatias ambledon Cope, 1866:294. No type locality specified.

Delphinus chilensis Philippi, 1895:283. Unavailable name, misidentification.

Tursio chiloensis Philippi, 1900:10, unlabeled illustration. Type locality is "no mui distante de Ancud" (translated as: not very far from Ancud [Chile]).

Lagenorhynchus australis: Kellogg, 1941:296. Name combination.

Lagenorhynchus cruciger (in part): Bierman and Slijper, 1947:1362. Name combination.

S[agmatias]. australis: LeDuc *et al.*, 1999:636, Figure 2. First use of current name combination.

Sagmatias australis: Moreno, 2008:23, Table 2. Name combination.

Cephalorhynchus australis: Moreno, 2008:79. Name combination.

HOLOTYPE

It is unknown what happened to the holotype of *Phocaena australis* from Peale (1849) after it was harpooned and secured aboard the vessel, but an excellent drawing was made from the specimen and appears as Plate 5, Figure 1 in Cassin (1858) where it was identified as *Delphinus obscurus*. Based on article 73.1.4 from the ICZN (1999), this drawing can serve as the designated holotype. According to Hershkovitz (1966), “type seen Feb. 12, 1839, but not preserved.”

TYPE LOCALITY

Peale (1849:33) provided only a short description and external measurements for the specimen that was “[h]arpooned in the South Atlantic Ocean, off the coast of Patagonia, on the 12th of February” (in the year 1839; see Wilkes 1845:107). A drawing was made of the specimen after it was secured and was to be printed on Plate 6 Figure 2 but the plates were not published in Peale’s volume (see Kellogg 1941). However, the drawing of the specimen was published by Cassin (1858:27, Plate 5 Figure 1), but neither Peale nor Cassin indicated whether the drawing was made by Peale or Joseph Drayon, the artist assigned to the *Vincennes* (two boats, the *Vincennes* and the *Peacock*, were part of the U.S. Exploring Expedition). Cassin, in his republication of Peale (1849) and using mostly Peale’s original description, synonymized *Phocaena australis* with *Delphinus obscurus* Gray, 1828. Based on various lines of evidence, Kellogg (1941) noted it is likely the skull and jaws used by Cope (1866) to describe *Sagmatias amblodon* were originally from the harpooned specimen. However, with the loss of some of Peale’s original notes and the lack/loss of associated collection history of Cope’s skull, whether these are two separate specimens or a single specimen will likely never be known (Kellogg 1941, Goodall *et al.* 1997c). Hershkovitz (1966) stated that the type locality of *P. australis* is “...one day’s sail north of the Straits of Le Maire between Staten Island and Cape San Diego, Tierra del Fuego” (Argentina), however, this detail does not appear in either Peale (1849) or Cassin (1858) but was included in Kellogg’s (1941:296) type description.

ETYMOLOGY

The species name *australis* is derived from Latin and means “southern,” referring to its occurrence within the southern waters of South America. The English common name, Peale’s dolphin, refers to Titian Ramsay Peale, an artist, explorer, and naturalist who served as

part of the scientific corps of the U.S. Exploring Expedition from 1838 to 1842 on the *Peacock*.

DIAGNOSIS

Among the four *Sagmatias* species, there are components of external pigmentation shared only among *S. australis*, *S. obscurus*, and *S. obliquidens*. Among these three similarly colored species there are three main pigmentation areas that differentiate *S. australis* from the others: (1) approximately posterior to the position of the eyes, *S. australis* has black lower lips, chin and throat coloration; (2) the flank patch is simple without the whitish dorsal and ventral flank blazes that are found on *S. obscurus*; and (3) there is an extension of white pigmentation in the abdominal field entering into the axilla ("armpit" region) of the flippers. Furthermore, there is no overlap in geographical distribution between *S. australis* and *S. obliquidens*. Additional features of *S. australis* coloration are given under *Coloration*.

In general, the skull morphology of all four species of *Sagmatias* is similar, except *S. australis* is unique in that the posterior end of the premaxillaries are developed into a flat and broad eminence and elevated posterior to the premaxillary foramina and to the anterior external bony nares (Kellogg 1941). This character is not found in any other species in the family Delphinidae. Both *S. australis* and *S. cruciger* can be distinguished from other *Sagmatias* species by having a smaller rostral length, longer braincase, and higher ramus (Miyazaki and Shikano 1997b). Furthermore, *S. australis* is differentiated from *S. cruciger* by having a smaller vertebral count, smaller external nares width, larger braincase, and narrower rostrum base width and external nares width (Miyazaki and Shikano 1997b).

Molecular data from both nuclear and mitochondrial DNA markers support the differentiation of *S. australis* from other species of *Sagmatias*, as well as from *Leucopleurus*, *Lagenorhynchus*, *Lissodelphis*, and *Cephalorhynchus* species (Fig. 2, 3). In these phylogenies, a close sister-species relationship is often recovered between *S. australis* and *S. cruciger*; however, the relationship between *S. australis* and *S. obliquidens*/*S. obscurus* is more uncertain and many of these studies have included little to no data from some of these species (Table 2; LeDuc *et al.* 1999, Harlin-Cognato and Honeycutt 2006, Agnarsson and May-Collado 2008, McGowen 2011, Banguera-Hinestroza *et al.* 2014a). Therefore, additional analyses may lead to further genus-level taxonomic revision for *S. australis*.

DISTRIBUTION

Sagmatias australis is endemic to southern South America and has the most restricted range of any species in this genus. Overall, the range of Peale's dolphins is mainly confined to the coastal waters in southern Chile and extending around Cape Horn into the South Atlantic along the coast of Argentina north to about the Rio de la Plata (between Argentina and Uruguay) and the coastal waters around the Falkland Islands (Fig. 1A). In marine biogeographic terms this region is known as the

Magellanic Province (Briggs 1974). Along the coast of Chile, the northernmost records are an incidental catch at San Antonio (33°35'S; Goodall *et al.* 1997c), and sightings just north of Valparaíso off the Aconcagua River, Concón (32°55'S) and Montemar (32°57'S; Aguayo 1975). However, this species is most common from Isla Grande de Chiloé (Isla Chiloé) and south to the waters of Chilean Patagonia which includes a vast complex of channels, islands, and fjords from 47°S to 57°S. In the western South Atlantic, the range of this species is more complex. The northernmost strandings are from the entrance of the Patos Lagoon, Brazil (33°42'S; Pinedo *et al.* 2002) and from Miramar, Argentina (38°17'S; Brownell 1974), and the northernmost sightings are from Peninsula Valdés (42°S; Crespo *et al.* 1997). Specimens and sightings are well documented from the Falkland Islands, typically in waters <200 m depth (Hamilton 1952, Strange 1992, White *et al.* 2002). However, offshore sightings are poorly documented except for a dolphin photographed 80 nmi offshore at 42°S, 62°W (Crespo *et al.* 1997).

Marginal localities—Although this species is mainly confined to the coastal zone, there have been occasional sightings over the Burdwood Bank (south of the Falkland Islands; White *et al.* 2002). A single sighting of a small group of dolphins in the South Pacific at Palmerston Atoll (18°S) that displayed coloration characteristic of the genus *Sagmatias* were tentatively identified as Peale's dolphins, but if they were indeed *S. australis* then the sighting is clearly extralimital (Leatherwood *et al.* 1991).

DESCRIPTION

Coloration—External morphological characteristics of *S. australis* include the presence of dark black or gray coloration on the dorsal surface with typically two lateral patches of lighter gray or white coloration: one extending from just behind the eye diminishing toward the ventral surface mid-body, and a second originating as a thin line just below the anterior portion of the dorsal fin extending along the caudal flank. The dorsal fin often has a darker anterior color and a lighter trailing edge. This species also has a black lower jaw, throat, and flippers, and a predominantly white ventral surface. The gray coloration of calves is typically lighter than that of adults (de Haro and Iñíguez 1997). Variations of *S. australis* pigmentation are further described in Goodall *et al.* (1997c).

Body form—*Sagmatias australis* has a robust body shape and a short rostrum that is not well-defined from the melon. The dorsal fin is mid-body, tall, and falcate. The presence of sexual dimorphism in terms of body size and length has not been confirmed for this species (Goodall *et al.* 1997c, Boy *et al.* 2011).

Meristics and osteology—*Sagmatias australis* has 26–37 upper and 27–36 lower teeth ($n = 24$; Table S1; Goodall *et al.* 1997c data from skulls) and a total vertebral count between 62 and 69 ($n = 37$; Table S1; Miyazaki and Shikano 1997b, Goodall *et al.* 1997c, Marchesi *et al.* 2017,

M. C. Marchesi^{22,23}). The skulls of 27 specimens had condylobasal lengths of 352–380 mm, mean 365.8 mm (Goodall *et al.* 1997c). The greatest total body length from 35 animals was 210 cm for adult females and 218 cm for adult males (Lichter 1992, Goodall *et al.* 1997c). Characteristics regarding physical maturity are not well known for this species. Goodall *et al.* (1997c) documented 26 specimens that had been assessed for physical maturity; of these, sex had been determined for 23. These included two physically mature females measuring 193 and 199 cm; however, there were four other females that ranged from 201 cm to 210 cm that were not yet physically mature. Of the six male specimens assessed, none were determined to be physically mature and included one neonate (138 cm) and five subadults (159–205 cm).

Variation (geographic or other)—Nothing is known about geographic variation within this species or any population-level differentiation among Chile, Argentina, and the Falkland Islands locations. Seasonal variation in abundance and sightings has been documented in the central Strait of Magellan, Chile where numbers increased during summer compared to winter months (Lescrauwaet 1997). In other areas throughout southern South America, additional records of seasonal variation in occurrence and abundance of *S. australis* have been reported but not substantiated (Goodall *et al.* 1997b).

Redescription of *Sagmatias cruciger* (Quoy and Gaimard, 1824)

COMMON NAME

Hourglass dolphin

SYNONYMY

Delphinus cruciger Quoy and Gaimard, 1824:87, Plate 11 Figures 3 and 4. Type locality is between “Nouvelle-Hollande et le cap Horn” (New Holland [Australia] and Cape Horn [Chile]).

Delphinus albigena Quoy and Gaimard, 1824:87, Plate 11 Figure 2. Type locality is close to New Holland (Australia) and Cape Horn, Chile as this specimen was collected “quelques jours après” (translated as: a few days after) *Delphinus cruciger* Quoy and Gaimard, 1824.

Delphinus bivittatus Lesson in Lesson and Garnot, 1827:178, Plate 9 Figure 3 (Atlas). Type locality is “Dans les mers orageuses du cap Horn, en allant aux Malouines, à cent quarante lieues de ces îles” (translated as: In the stormy seas of Cape Horn, on the way to the Falklands, a hundred and forty leagues from these islands).

Phocaena Homeii Smith, 1829:440. Type locality is “the seas about the Cape of Good Hope.”

²²Personal communication from María Constanza Marchesi, Centro Austral de Investigaciones Científicas (CADIC-CONICET). Bernardo Houssay 200, CP, V9410BFD, Ushuaia, Argentina, 10 July 2017.

²³See note 11 above.

- Delphinus livitatus* F. Cuvier, 1836:225. Incorrect subsequent spelling. *D[elphinus]. albigenus*: Gray, 1846b:44. Justified emendation, correction of gender agreement.
- Lagenorhynchus clanculus* Gray, 1846b:Plate 35. No type locality specified, but listed as “Pacific” by Gray (1849, 1850b).
- D[elphinus]. bivittatus*: Gay, 1847:175. Name combination.
- D[elphinus]. cruciger*: Gay, 1847:175. Name combination.
- Delphinus obscurus*: Gray, 1850a:107. Name combination.
- Electra clancula*: Gray, 1868b:7, Plate 35. Name combination.
- Electra crucigera*: Gray, 1871:77. Name combination.
- Lagenorhynchus cruciger*: Van Bénédén and Gervais, 1880:598, Plate 36 Figure 3. Name combination.
- Lagenorhynchus latifrons* True, 1889:84, 90. No type locality specified.
- Phocaena d’Orbigny* Philippi, 1893:10, Plate 2 Figure 2 (“*Phocaena D’Orbigny* Ph.”). No type locality specified.
- Phocaena crucigera*: Philippi, 1893:11, Plate 3 Figure 4 (“*Ph. bivittata* Lesson”) and Figure 5 (“*Ph. crucigera* Quoy et Gaim.”). Name combination.
- Tursio obscurus*: Gray, 1866a (Philippi 1896):17. Name combination.
- Lagenorhynchus Fitzroyi*: Lahille, 1899:200. Unavailable name, misidentification.
- Lagenorhynchus wilsoni* Lillie, 1915:123. No type locality specified, but it “would seem to be confined to a comparatively narrow band of the Southern Ocean, just north of the pack-ice, between Lat. 65°S. and Lat. 54°S.”
- L[agenorhynchus]. cruciger*: Yañez, 1948:115. Name combination.
- Sagmatias cruciger*: LeDuc et al., 1999:636, Figure 2. First use of current name combination.
- Cephalorhynchus cruciger*: Moreno, 2008:79. Name combination.

HOLOTYPE

Since the naming authority belongs to Quoy and Gaimard (1824) and is based on figures drawn from sighting animals at sea, the holotype for *S. cruciger* is designated as Figures 3 and 4 from Plate 11 (Atlas; Quoy and Gaimard 1824), following article 73.1.4 from the ICZN (1999). True (1889:90) incorrectly stated that the holotype specimen is in the “Paris Museum, No. a3045, labeled *L. cruciger*, d’Orbigny, 1830 (type),” and we know of no “d’Orbigny, 1830” publication. This mistake was reiterated by Robineau (1990) in his list of cetacean types in the Paris Museum.

TYPE LOCALITY

Quoy and Gaimard (1824) first sighted *S. cruciger* between “Nouvelle-Hollande et le cap Horn” (New Holland [Australia] and Cape Horn [Chile]) in January of 1820 around 49°S. The first specimen was collected “du 57° au 76° degré de latitude sud, ou à l’est et au sud du Cap Horn” (from 57°S to 76°S latitude, or east and south of Cape Horn [Chile]; d’Orbigny and Gervais 1847).

ETYMOLOGY

The species name *cruciger* is derived from the Latin words *crucis* meaning “a cross” and *gerous* meaning “bearing,” referring to their black coloration which from above may resemble a Maltese cross. The English common name, hourglass dolphin, refers to their distinctive lateral white blazes that resemble an hourglass pattern.

DIAGNOSIS

Sagmatias cruciger has a distinctive black and white pigmentation pattern that easily distinguishes it from the other three *Sagmatias* species—laterally there are two distinct white blazes (which are often connected by a thin white line) that separate areas of black coloration. Additional features of *S. cruciger* coloration are given under *Coloration*.

In general, the skull morphology of all four species of *Sagmatias* is similar, however, both *S. australis* and *S. cruciger* can be distinguished from other *Sagmatias* species by their shorter rostral length, longer braincase, and higher ramus (Miyazaki and Shikano 1997b). Furthermore, *S. cruciger* is differentiated from *S. australis* by its greater width of external nares and rostrum base and its smaller braincase (Miyazaki and Shikano 1997b). *Sagmatias cruciger* has a larger vertebral count and its vertebrae are smaller in overall size compared to those of *S. australis* (Goodall *et al.* 1997a, Miyazaki and Shikano 1997b).

Molecular data from both nuclear and mitochondrial DNA markers support the differentiation of *S. cruciger* from the other species of *Sagmatias*, *Leucopleurus*, *Lagenorhynchus*, *Lissodelphis*, and *Cephalorhynchus* (Fig. 2, 3). In these phylogenies, a close sister-species relationship is often recovered between *S. cruciger* and *S. australis*; however, the relationship between *S. cruciger* and *S. obliquidens*/*S. obscurus* is less clear and studies often have included little to no data from some of these species and particularly *S. cruciger* (Table 2; LeDuc *et al.* 1999, Harlin-Cognato and Honeycutt 2006, Agnarsson and May-Collado 2008, McGowen 2011, Banguera-Hinestroza *et al.* 2014a). Thus, genus-level taxonomic revision may be necessary for *S. cruciger* consequent on additional analyses.

DISTRIBUTION

Sagmatias cruciger has a circumpolar distribution in offshore waters of the Southern Hemisphere typically between 43°S and 67°S (most often between 54°S and 62°S) on either side of the Antarctic Convergence (Fig. 1A) and, apart from killer whales, is the only other delphinid commonly found south of the Antarctic Convergence. Kasamatsu and Joyce (1995) found that *S. cruciger* occurred most often in the northernmost waters of the Antarctic. The northern- and southernmost sightings occurred off Chile (33°40'S, 74°55'W; Clarke 1962) and in the South Pacific (67°38'S, 179°57'E; Kasamatsu *et al.* 1988, Miyazaki and Kato 1988, Brownell and Donahue 1999), respectively. However, the Clarke (1962) sighting has been questioned by Goodall *et al.* (1997a) and we too doubt that the Clarke sighting was of *S. cruciger*. It is much

more likely these dolphins were *S. obscurus* in this location. Thus, the sightings of Murphy (1947) from 42°24'S, 42°28'W (>1,300 km north of South Georgia) and Nichols (1908) from 36°14'S, 52°43'W (off Argentina) are the northernmost records. Off southeastern South America, sightings have been clustered on the edge of the shelf off South Georgia and in the deep waters of the Drake Passage (Goodall 1997). This species has been recorded on numerous occasions around the Falkland Islands, typically in water >200 m deep (White *et al.* 2002). Sightings and strandings have also been reported at the Kerguelen Islands (Robineau 1989).

Marginal localities—We consider a recent sighting of an hourglass dolphin along with three Peale's dolphins in inland waters of Parry fjord, Tierra del Fuego Island, Chile an atypical occurrence (Acevedo *et al.* 2017).

DESCRIPTION

Coloration—External morphological characteristics of *S. cruciger* include a predominantly black body with two distinct lateral white blazes often connected by a thin white line: one blaze extending from in front of and above the eye, thinning toward mid-body below the dorsal fin, and a second blaze originating just below the dorsal fin and extending the length of the caudal flank. The demarcation between dark black/gray and white areas is very sharp. The dorsal fin, flippers, fluke and tip of the upper and lower jaws are black, and the ventral surface is predominantly white or gray. Variations of *S. cruciger* pigmentation are further described and illustrated in Goodall *et al.* (1997a) and Jefferson *et al.* (2015).

Body form—The body shape of *S. cruciger* is less robust than that of other *Sagmatias* species, it has a small rostrum that is clearly defined from the melon, and the tailstock has a noticeable postanal hump that is more developed in males compared to females (Brownell and Donahue 1999, Best 2007). The dorsal fin is mid-body, large, and curved. A large variation in dorsal fin shape has been reported by observers and documented in Goodall (1997). The shape ranges generally from a tall, slanted, pointed fin to one that is tall, hooked, and rounded at the tip. It is unclear if variation in dorsal fin shape is significantly correlated with any other characteristics such as sex, age, or geography. However, the dorsal fins that are the most hooked in shape (in dolphins of known sex) have been from adult males (Best 2007). Furthermore, sexual dimorphism in terms of body size and length has not been documented for this species, although the overall sample size of available specimens for this species is very small (<20).

Meristics and osteology—Internal morphological characteristics include the presence of 27–35 upper and 27–31 lower teeth ($n = 7$; Goodall *et al.* 1997a data from skulls; Gazitúa *et al.* 1999) and a total vertebral count of 65–72 ($n = 15$; Goodall *et al.* 1997a, Marchesi *et al.*

2017).²⁴ The skulls of 16 specimens had condylobasal lengths of 316–370 mm (True 1889, Goodall *et al.* 1997a, Gazitúa *et al.* 1999). Total body lengths have been recorded for 12 specimens: six females ranging from 142 cm to 182.9 cm and six males from 162.6 cm to 187 cm (Miyazaki 1986, Goodall *et al.* 1997a, Brownell and Donahue 1999, Fernández *et al.* 2003). Of these 12 specimens, the largest female was 182.9 cm and nearing sexual maturity (with some epiphyses unfused; Fraser 1966, Goodall *et al.* 1997a), the largest reported sexually mature male was 178 cm (Fernández *et al.* 2003), and the largest male reported to date (187 cm) was a subadult with some epiphyses unfused (Goodall *et al.* 1997a).

Variation (geographic or other)—Kasamatsu and Joyce (1995) reported possible seasonal variation in density for *S. cruciger* and found that densities (recorded from November to February) started increasing in waters south of 60°S in early February and continued until the end of the survey at the end of the month. The authors speculated that this pattern was correlated to increases in sea surface temperature. A potential northward migration towards New Zealand waters during winter months was suggested by Gaskin (1972). Seasonal variation in occurrence has also been documented around the Falkland Islands, where *S. cruciger* is sighted most often from September to March (White *et al.* 2002).

Redescription of *Sagmatias obliquidens* (Gill, 1865)

COMMON NAME

Pacific white-sided dolphin

SYNONYMY

Lagenorhynchus obliquidens Gill, 1865:177. Type locality is “San Francisco, California.”

Delphinus longidens Cope, 1866:295. No type locality specified.

Clymenia similis Gray, 1868b:6. Unavailable name, misidentification.

Lagenorhynchus longidens: True, 1889:99. Name combination.

Lagenorhynchus ognevi Sleptsov, 1955:60, Figures 1–3. Type locality is “in the Nemoro Sea, 15–20 miles east of the South Kuril Cape (Kunashir Island)” (Russia/Japan).

(*S[agmatias].*) *obliquidens*: LeDuc *et al.*, 1999:639, Figure 2. First use of current name combination.

Sagmatias obliquidens: Moreno, 2008:23, Table 2. Name combination.

HOLOTYPE

The three skulls of *Lagenorhynchus obliquidens* Gill, 1865, collected by W. P. Trowbridge, exist as syntypes (USNM 1961, 1962, and 1963) in

²⁴See note 11 above.

the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Fisher and Ludwig 2016).

TYPE LOCALITY

Gill (1865:178) states that the skulls mentioned above were “obtained at San Francisco, California.”

ETYMOLOGY

The species name *obliquidens* is derived from the Latin words *obliquus* meaning “slanting” and *dens* meaning “tooth.”

DIAGNOSIS

Sagmatias obliquidens is the only species of *Sagmatias*, *Leucopleurus*, *Lagenorhynchus*, or *Cephalorhynchus* that inhabits the North Pacific Ocean. Among *Sagmatias*, *Lagenorhynchus*, and *Leucopleurus* species, the pigmentation of *S. obliquidens* is similar to that of *S. obscurus* and *S. australis*, however there is no overlap in distribution between *S. obliquidens* and either of these two species. Fraser (1966) stated that the pigmentation pattern of *S. obliquidens* is most similar to that of *S. australis*, but these two species can be distinguished based on the extent of dark pigmentation on the chin and the pattern of the flank patch at the posterior flipper insertion, and the dorsal fin of *S. obliquidens* is often lighter with more gray pigmentation than that of *S. australis*. Additional features of the coloration of *S. obliquidens* are given under *Coloration*.

In general, the skull morphology of all four species of *Sagmatias* is similar, however *S. obliquidens* and *S. obscurus* can be distinguished from other *Sagmatias* species by their greater rostral length, shorter braincase, and lower ramus (Miyazaki and Shikano 1997b). Furthermore, *S. obliquidens* is differentiated from *S. obscurus* by having a greater preorbital width and a wider rostrum at midlength (Miyazaki and Shikano 1997b). *Sagmatias obliquidens* also has more vertebrae than *S. obscurus* (Miyazaki and Shikano 1997b).

The distinction between *S. obliquidens* and the other species of *Sagmatias* as well as all species in the genera *Leucopleurus*, *Lagenorhynchus*, *Lissodelphis*, and *Cephalorhynchus* is also supported by genetic data from both nuclear and mitochondrial DNA markers (Fig. 2, 3). Phylogenetic studies consistently recover a close sister-species relationship between *S. obliquidens* and *S. obscurus*, but the relationships between *S. obliquidens* and *S. australis*/*S. cruciger* are less clear and these studies often have included little to no data from the latter two species (Table 2; Harlin-Cognato and Honeycutt 2006, May-Collado and Agnarsson 2006, Agnarsson and May-Collado 2008, McGowen 2011, Banguera-Hinestroza *et al.* 2014a). Additional analyses may lead to further genus-level taxonomic revision for *S. obliquidens*. If *S. obliquidens* and *S. obscurus* are determined to be significantly differentiated at the genus level from *S. australis* and *S. cruciger*, a new genus name will be needed for *obliquidens* and *obscurus* because *S. amblodon* Cope, 1866 (= *australis*) is the type

species of *Sagmatias* and no other synonyms are available for these two species.

DISTRIBUTION

Sagmatias obliquidens inhabits the cold-temperate waters of the North Pacific between 20°N and 60°N (Fig. 1A). In the western Pacific, it ranges from the East China Sea, throughout Japanese waters including the Sea of Japan, and around the Kuril and Commander Islands, and eastward into the Aleutian Islands (Sleptsov 1955, Huang and Tang 1979, Wang 1985, Miyazaki 1983, Brownell *et al.* 1999b). This species also has been recorded in the southwestern Okhotsk Sea and the south-eastern Bering Sea (Kajimura and Loughlin 1988, Miyashita and Berzin 1991). In the eastern Pacific, it ranges along the continental shelf and slope from Baja California Sur, Mexico northward along the west coast of North America to the Gulf of Alaska, and west to Amchitka in the Aleutian Islands (Leatherwood *et al.* 1984, Walker *et al.* 1986, Stacey and Baird 1991, Mangels and Gerrodette 1994, Barlow 2016). *Sagmatias obliquidens* also occurs in inland waterways of southeastern Alaska (Leatherwood *et al.* 1984, Dahlheim and Towell 1994) and in oceanic waters of the North Pacific between 38°N and 47°N (Hobbs and Jones 1993, Iwasaki and Kasuya 1997).

Marginal localities—Zhou (2004) provides an illustration and measurements of a skull from Fudan University, Shanghai (specimen #46) collected from the western side of the East China Sea (see p.176, Fig. 91). This same skull is pictured in Wang (1999; p. 263, Fig. 30-2). This specimen can be identified as *S. obliquidens* based on these images, and this occurrence represents the southern limit in the East China Sea. A report of this species from the Gulf of Tonkin (Wang 1985, Zhou 2004) is likely a misidentification as it is well beyond its normal range, and *S. obliquidens* has never been found in Taiwanese waters (Yang 1976, Zhou *et al.* 1995, Wang and Yang 2007, J. Y. Wang²⁵) where small cetaceans are well studied.

DESCRIPTION

Coloration—*Sagmatias obliquidens* is characterized by dark gray or black coloration on the dorsal and lateral sides of the body. The dark areas are interrupted dorsally by a thin gray line, reminiscent of “suspenders,” that extends from above the eye widening into a light gray caudal blaze posterior to the dorsal fin. Anteriorly, a light gray thoracic patch extends from the front of and above the eye to mid-body below the dorsal fin. The belly is white and separated from the darker lateral areas by a black line. The upper jaw and lower lips are black. Both the dorsal fin and flippers are shaded dark gray on the anterior edge and light gray posteriorly. Numerous studies have reported color variants of *S. obliquidens* across the North Pacific (*e.g.*, Walker *et al.* 1986,

²⁵Personal communication from John Y. Wang, CetAsia Research Group. 310-7250 Yonge Street, Thornhill, Ontario L4J-7X1, Canada, 24 July 2018.

Sekiguchi *et al.* 2014, Jefferson *et al.* 2015). Predominantly white individuals (non-albino) with varying degrees of a lack of pigmentation have been observed off Baja California, California, and Japan (Brown and Norris 1956, Hain and Leatherwood 1982, Stacey and Baird 1991, Black 1994, Tsutsui *et al.* 2001). Brownell (1965) described an anomalous color pattern where animals have a large, dark black thoracic area and a distinct white stripe between the dark thoracic area and the dark dorsal back. Often the white stripe extends over the eye. This “Brownell-type” color pattern has since been documented across the North Pacific; however, despite high survey effort this pattern has never been reported around Japan (Sekiguchi *et al.* 2014).

Body form—The body shape of *S. obliquidens* is robust with a short rostrum that is not obviously differentiated from the melon. The large dorsal fin is positioned mid-body and the shape is variable across the species’ range, from sharply falcate to heavily lobate (Walker *et al.* 1986, Brownell *et al.* 1999b, Morton 2000). The presence of a large, lobate dorsal fin may be correlated with age (Walker *et al.* 1986). No evidence of sexual dimorphism in total body length has been found in a large sample of animals from the Pacific high seas ($n > 300$; Ferrero and Walker 1996) or around Iki Island, Japan ($n > 50$; Miyazaki and Shikano 1997a).

Meristics and osteology—Internal morphological characteristics include the presence of 25–34 upper and 25–33 lower teeth ($n = 28$; Table S1) and a total vertebral count between 74 and 78 ($n = 15$; Miyazaki and Shikano 1997b).²⁶ The skulls of 144 sexually mature specimens from the eastern North Pacific had condylobasal lengths of 350–446 mm (Walker *et al.* 1986). In the western North Pacific, condylobasal lengths of animals 4.5 yr of age or older measured 363–433 mm ($n = 25$: females) and 375–439 mm ($n = 19$: males; Miyazaki and Shikano 1997a). In the eastern North Pacific, the largest documented total body lengths for female and male specimens were 236 cm and 250 cm, respectively ($n = 243$; Walker *et al.* 1986). In Japanese waters, the largest female and male were reported as 229 cm and 238 cm, respectively ($n = 174$; Kasuya 1985). In the central North Pacific between 38°N and 46°N, the largest female and male were 230 cm and 237 cm, respectively ($n = 341$; Ferrero and Walker 1996; $n = 242$; Iwasaki and Kasuya 1997).

Variation (geographic or other)—Multiple morphological, genetic, and acoustic variants, as well as variations in movement patterns, have been identified for *S. obliquidens* and have been described as follows:

Western North Pacific: Specimens from Iki Island (Korea Strait, southwestern Japan) were significantly longer in total body length and condylobasal length and larger in over 20 cranial characteristics compared to animals in offshore North Pacific waters (Miyazaki and Shikano 1997a).

²⁶See note 11 above.

Consistent with these morphological findings, genetic evidence based on both mitochondrial and nuclear DNA supports that animals from coastal Japanese waters are genetically distinct from those in offshore waters (Hayano *et al.* 2004).

Possible seasonal variation in movement has been documented around Japan, where *S. obliquidens* has been observed around the southwest coast in winter months and in northeastern coastal waters from spring into summer (Kasuya 1971).

Eastern North Pacific: In California, animals collected from north of 37°N ($n = 50$) had significantly shorter condylobasal lengths than those from below 32°N ($n = 10$)—approximately ≤ 400 mm for northern and > 400 mm for southern animals (Walker *et al.* 1986). Also, northern animals had shorter total body lengths compared to southern animals—approximately ≤ 210 cm for northern and > 210 cm for southern animals (Walker *et al.* 1986). Furthermore, there was significant variability in cranial characters of animals collected between these two areas, and particularly in the Southern California Bight, suggesting an area of mixing between a smaller northern and larger southern morphological form (Walker *et al.* 1986).

Both mitochondrial and nuclear DNA evidence indicates that these two morphological forms represent genetically distinct populations (Lux *et al.* 1997; NLV, unpublished data). Furthermore, these data support the presence of three genetically distinct populations in the eastern North Pacific: (1) a population ranging from Baja California Sur north into the Southern California Bight; (2) a population ranging from around the Southern California Bight north to the U.S.–Canada border and ranging west into the high seas ($\sim 165^\circ\text{W}$); and (3) a population off the west coast of Canada and throughout the Gulf of Alaska (Lux *et al.* 1997; NLV, unpublished data).

Additionally, two acoustic variants (differing in echolocation click type) have been identified: a northern and a southern variant that overlap within the Southern California Bight (Soldevilla *et al.* 2010). Seasonal movements (described below) of both variants suggest that they represent the morphological/genetic variants described above. The animals using the two acoustic variants also differ in behavior and vocalization patterns, and niche partitioning may be occurring between the two overlapping populations (Henderson *et al.* 2011).

Pacific white-sided dolphins are more abundant in shelf waters off Oregon and Washington in the late spring and off southern California during the winter and early spring (Forney *et al.* 1995, Forney and Barlow 1998, Barlow 2016). Soldevilla *et al.* (2010) suggested that in the Southern California Bight the northern acoustic variant moves north and offshore in the spring and summer, and south and inshore during the fall and winter, while the southern variant moves north into the Bight during the fall and winter, and south into Mexican waters during the spring and summer. In inshore southwestern Alaska waters, *S. obliquidens* was found to occur more frequently in spring months, possibly correlated with periods of warmer water (Dahlheim and Towell 1994, Dahlheim *et al.* 2009). Further south, inshore of Vancouver Island, the species was observed more frequently in winter months (Morton 2000). Aurioles *et al.* (1988) reported that

S. obliquidens was present off Baja California Sur in the spring and early summer. However, the occurrence of Pacific white-sided dolphins has decreased in this area since the 1980s, a trend that may be related to warming water temperature as a result of global climate change (Salvadeo *et al.* 2010).

Redescription of *Sagmatias obscurus* (Gray, 1828)

COMMON NAME

Dusky dolphin

SYNONYMY

Delphinus superciliosus Lesson in Lesson and Garnot, 1827:181, Plate 9 Figure 2 (Atlas). Nomen dubium.

Phocœna superciliosa: Lesson, 1827:415. Name combination.

Delphinus (Grampus) obscurus Gray, 1828:2, Plate 2 Figures 2–5. Type locality is “Cape of Good Hope” (South Africa).

Delphinus obscurus (variété): Quoy and Gaimard, 1830:151, Plate 28 Figure 2. Type locality is “le cap de Bonne-Espérance” (Cape of Good Hope), South Africa.

Delphinus Fitzroyi Waterhouse, 1838:23. Type locality is “in the Bay of St. Joseph” and “coast of Patagonia, Lat. 42°30’” (off Argentina).

Delphinus breviceps Wagner, 1846:427, Plate 368 Figure 1. No type locality specified but is stated as “Rio de la Plata” (Argentina) by Jacquinot and Pucheran (1853).

Delphinus obscurus: Gray, 1846b:37, Plate 16. Name combination.

Lagenorhynchus? nilssonii Gray, 1864:238. Unavailable name, mis-identification.

Tursio obscurus: Gray, 1866a:264. Name combination.

Lagenorhynchus breviceps: Gray, 1866a:271. Name combination.

Clymene obscura: Gray, 1866b:215. Name combination.

D[elphinus]. (Tursio) obscurus: Cope, 1866:295. Name combination.

Delphinus (Tursio) obscurus: Burmeister, 1867:306. Name combination.

Clymene similis Gray, 1868a:146, Figure 2. Type locality is “Cape of Good Hope (*Layard*)” (South Africa).

Clymenia obscura Gray, 1868b:6, Plate 16. Unjustified emendation.

Clymenia similis Gray, 1868b:6. Unjustified emendation.

Clymenia]. obscura: Gray, 1870:393, 394. Name combination.

Electra breviceps: Gray, 1871:76. Name combination.

Lagenorhynchus fitzroyi: Flower, 1885:23. Name combination.

Prodelphinus obscurus: Flower, 1885:28. Name combination.

Prodelphinus superciliosus: Jentink, 1887:173. Name combination.

Prodelphinus Petersii Lütken, 1889:43. No type locality specified.

Lagenorhynchus superciliosus: True, 1889:92, Plate 25 Figure 3. Name combination.

Lagenorhynchus obscurus: True, 1889:104, Plate 29 Figures 1 and 2. Name combination.

- Lagenorhynchus obscurum* Blanford, 1891:580. Type locality is “Palk Straits, Ceylon” (Sri Lanka).
- Phocaena posidonia* Philippi, 1893:9, Plate 2 Figure 1. Type locality is “48°10' latit. sur i 77° lonjit. oeste” (48°10' latitude south and 77° longitude west) off Chile.
- Phocaena fitzroyi*: Philippi, 1893:13, Plate 5 Figure 2. Name combination.
- Tursio? Panope* Philippi, 1895:284. No type locality specified.
- Lagenorhynchus thicola breviceps*: Trouessart, 1898-1899:1038. Name combination.
- Lagenorhynchus Fitzroyi*: Lahille, 1899:200. Name combination.
- [*Lagenorhynchus*]. *posidonia*: True, 1903:137, 138. Name combination.
- Lissodelphis? panope*: Trouessart, 1904:766. Name combination.
- Lagenorhynchus superciliosus* Trouessart, 1904:767. Incorrect subsequent spelling.
- [*Lagenorhynchus*]. *obscurus*: Schneider, 1946:80. Name combination.
- Lagenorhynchus fitzroyi* Bini, 1951:91, Figures 12 and 13. Incorrect subsequent spelling.
- (*Sagmatias*) *obscurus*: LeDuc *et al.*, 1999:639, Figure 2. First use of current name combination.
- Sagmatias obscurus*: Mann *et al.*, 2000:348, Appendix 2. Name combination.

HOLOTYPE

According to the online catalog of the British Museum (Natural History), London (accessed 21 July 2017), the holotype of *Delphinus (Grampus) obscurus* Gray, 1828 exists at this museum as a skull with the catalog no. 1841.1733. However, additional specimens are cataloged under the same number. These presumably refer to the “young,” “adult,” and/or “Crania” specimens referenced by Gray (1828:2). For the “Type of species,” Flower (1885:28) states “*a*. Stuffed specimen; and skull removed from the same in 1884. (41.1733) Cape of Good Hope (*Capt. Heaviside*). Transferred from the Museum of the Royal College of Surgeons (1841). Type of species. Described and figured, *loc. cit.* pl. ii. fig. 3.”

TYPE LOCALITY

The holotype of *Delphinus (Grampus) obscurus* Gray, 1828 has a type locality of “Cape of Good Hope.”

ETYMOLOGY

The species name *obscurus* is derived from Latin and means “dark.”

DIAGNOSIS

Among *Sagmatias*, *Lagenorhynchus*, and *Leucopleurus* species, the pigmentation of *S. obscurus* is most similar to that of *S. obliquidens* and *S. australis*, however only *S. obscurus* and *S. australis* overlap in distribution (*i.e.*, off southern South America; Fig 1A). In contrast to *S. obliquidens*, the dorsal flank blaze of *S. obscurus* does not extend further anteriorly than mid-body (Van Waerebeek and Würsig 2018). *Sagmatias obscurus* can be distinguished from *S. australis* by the former

having an extension of the light-colored thoracic patch over the eye (Reeves *et al.* 2002). In the southern portion of its range, *S. obscurus* may be confused with *S. cruciger*; however, the two can be differentiated based on the sharply defined light and dark areas, broad dorsal fin shape, and dark pigmentation behind the flipper that is characteristic of *S. cruciger* (Reeves *et al.* 2002). Additional features of *S. obscurus* pigmentation are given under *Coloration*.

In general, the skull morphology of all four species of *Sagmatias* is similar, however *S. obscurus* and *S. obliquidens* can be distinguished from other *Sagmatias* species by having a longer rostrum, shorter braincase, and lower ramus (Miyazaki and Shikano 1997b). Furthermore, *S. obscurus* is differentiated from *S. obliquidens* by having a narrower preorbital width and narrower width of the rostrum at midlength (Miyazaki and Shikano 1997b). *Sagmatias obscurus* also has fewer vertebrae than *S. obliquidens* (Miyazaki and Shikano 1997b).

The distinction between *S. obscurus* and the other species of *Sagmatias* as well as all of the species in the genera *Leucopleurus*, *Lagenorhynchus*, *Lissodelphis*, and *Cephalorhynchus* is also supported by genetic data from both nuclear and mitochondrial DNA markers (Fig. 2, 3). Phylogenetic studies consistently recover a close sister-species relationship between *S. obscurus* and *S. obliquidens*, but the relationship between *S. obscurus* and *S. australis*/*S. cruciger* is less clear and these studies often have included little to no data from the latter two species (Table 2; Harlin-Cognato and Honeycutt 2006, May-Collado and Agnarsson 2006, Agnarsson and May-Collado 2008, McGowen 2011, Banguera-Hinestroza *et al.* 2014a). Further genus-level taxonomic revision may be necessary for *S. obscurus*; however, any changes are contingent on additional data and analysis. If *S. obscurus* and *S. obliquidens* are determined to be significantly differentiated at the genus level from *S. australis* and *S. cruciger*, a new genus name will be needed for the former two species as no other synonyms are available for *S. obscurus* and *S. obliquidens* and *S. amblodon* Cope, 1866 (= *australis*) is the type species of *Sagmatias*.

DISTRIBUTION

Sagmatias obscurus inhabits coastal and shelf areas discontinuously throughout the Southern Hemisphere (Fig. 1A). It rarely occurs along the southeast coast of Australia and around Tasmania (Gill *et al.* 2000), and species identifications from sightings south of Australia (*e.g.*, Lillie 1915) have been questioned (Gaskin 1972, Baker 1999, Gill *et al.* 2000, Van Waerebeek *et al.* 1995). We too do not accept these observations for two reasons: (1) they could easily have been confused with *S. cruciger*, and (2) the location is on the high seas at or below the Antarctic Circumpolar Current which is well outside the normal range of *S. obscurus*. However, *S. obscurus* is well documented in New Zealand waters, including around the South Island and the southern and central portions of the North Island up to East Cape on the east coast and to the Taranaki Bight and off Cape Egmont along the west coast (Cipriano and Webber 2010). To the east, *S. obscurus* is also found around the Chatham Islands, and to the south

around Campbell and Auckland Islands (Gaskin 1968, 1972; Baker 1977, 1999; Webber 1987; Würsig *et al.* 1997, 2007).

In South America, the northernmost west coast specimens are from Peru, from Chimbote ($9^{\circ}05'S$) and Salaverry ($\sim 8^{\circ}S$; Van Waerebeek 1992, Van Waerebeek *et al.* 1997a, Reyes 2009) and the northernmost east coast sighting location is Porto Alegre, Brazil ($\sim 30^{\circ}S$; Würsig *et al.* 1997). A possible gap in distribution was reported by Van Waerebeek (1992) along the coast of Chile between $36^{\circ}30'S$ and $46^{\circ}S$, however, several sightings have been documented from this area (Goodall *et al.* 1997b) and Cipriano and Webber (2010) suggest that the distribution is indeed continuous from central Peru into Chile. Along Argentina, *S. obscurus* is regularly found from Mar del Plata south to Puerto Deseado (*e.g.*, Würsig and Bastida 1986, Crespo *et al.* 1997, Schiavini *et al.* 1999), and occasionally south to Tierra del Fuego with the southernmost records south of Cape Horn ($\sim 57^{\circ}S$ – $60^{\circ}S$; Goodall *et al.* 1997b). Specimens of *S. obscurus* have been collected from the Falkland Islands (Islas Malvinas) and sighted in these waters thus confirming the species' occurrence there, although these dolphins are not abundant in the Falklands (Van Waerebeek *et al.* 1995). In fact, during a 3 yr survey period between 1998 and 2001 around the Falkland Islands, no dusky dolphins were observed (White *et al.* 2002).

Sagmatias obscurus also inhabits the coastal waters of southwestern Africa, from at least as far north as Walvis Bay, Namibia ($\sim 23^{\circ}S$; and possibly farther north to Angola $\sim 12^{\circ}S$) and south to False Bay, South Africa ($\sim 19^{\circ}E$; Findlay *et al.* 1992, Best 2007, Elwen *et al.* 2010). Findlay *et al.* (1992) reported a hiatus in distribution from $27^{\circ}S$ to $30^{\circ}S$ and also between $21^{\circ}S$ and $23^{\circ}S$, with the former break potentially related to the presence of the Namaqua upwelling cell.

Finally, *S. obscurus* has been documented around several oceanic islands in the South Atlantic and Indian Ocean. Specifically, the species has been verified at Gough Island in the South Atlantic and at Amsterdam Island (and presumably at nearby St. Paul Island) and the Prince Edward Islands in the southern Indian Ocean (Kasamatsu *et al.* 1990, Van Waerebeek *et al.* 1995). Although there have been reports of *S. obscurus* around the Crozet and Kerguelen Islands, species identifications were either found to be incorrect (*e.g.*, Robineau (1989) confirmed a potential *S. obscurus* Kerguelen specimen as *Cephalorhynchus commersonii*) or have not been confirmed (Van Waerebeek *et al.* 1995).

Marginal localities—On the east coast of South America, the northernmost sighting is off Porto Alegre, Brazil ($\sim 30^{\circ}S$; Würsig *et al.* 1997). However, we consider this record as extralimital as there are no subsequent sightings from southernmost Brazil or Uruguay.

DESCRIPTION

Coloration—The color pattern of *S. obscurus* is dark gray or black on the dorsal side and white ventrally. Laterally, there are two light gray patches: a thoracic patch extending over and in front of the eye, and a two-pronged blaze mid-body and along the flank. The coloration of the thoracic patch can also extend to the flippers. The beak is dark and the

dorsal fin has a dark leading edge and a lighter-colored trailing edge. Animals with an anomalous piebald pigmentation pattern have been observed in Peru and South Africa (Van Waerebeek 1993a). Additionally, a darker form has been reported from Peninsula Valdés, Argentina (pictured in Würsig and Würsig 1979) with black upper and lower lips, black eye patches, an almost entirely black dorsal fin, and some yellow-brown pigmentation at the interface of light and dark areas (Cipriano and Webber 2010). This darker form may be similar to the specimen described from Mar del Plata, Argentina (Gallardo 1912) and the “Fitzroy form” discussed by Van Waerebeek (1993a). A lighter phenotype was also described by Van Waerebeek (1993a).

Body form—*Sagmatias obscurus* has a moderately robust body shape and a short, stubby rostrum that is not particularly noticeable. The dorsal fin is mid-body, tall, and falcate. The dorsal fin of males in Peruvian waters has a broader base and is more strongly curved than that of females, however sex cannot be determined in the field based on this character alone (Van Waerebeek 1993a). Furthermore, there is no sexual dimorphism in total body length (Van Waerebeek 1993a).

Meristics and osteology—Based on the discontinuous distribution of *S. obscurus*, morphological characteristics have been categorized based on locality of specimens²⁷:

Argentina: There are not much data available from this region. Dans *et al.* (1997) collected 18 female specimens that ranged in total body length from 157 cm to 174 cm.

Peru/Chile: Animals have 26–39 ($n = 124$) upper and 26–37 ($n = 119$) lower teeth (Van Waerebeek 1993b) and a total vertebral count between 73 and 74 ($n = 2$; Van Waerebeek *et al.* 1995). The largest documented total body length for female ($n = 26$) and male ($n = 14$) specimens was 204.5 cm and 206 cm, respectively (Manzanilla 1989). In Peruvian animals, skulls from 59 females had condylobasal lengths of 368–426 mm, and 49 males measured 372–420 mm (Van Waerebeek 1993b).

South Africa: Animals have 26–32 upper and 24–31 lower teeth ($n = 106$; Best 2007) and a total vertebral count between 71 and 75 ($n = 49$; Best 2007). The largest documented total body length for female ($n = 53$) and male ($n = 51$) specimens was 191 cm and 190 cm, respectively (Best and Meÿer 2010). Skulls from 34 animals had condylobasal lengths of 342–386 mm (Van Waerebeek 1993b).

New Zealand: Animals have 28–37 upper ($n = 37$) and 27–39 ($n = 40$) lower teeth (Van Waerebeek 1993b) and a total vertebral count between 69 and 72 ($n = 8$; Van Waerebeek *et al.* 1995). The largest documented total body length of female ($n = 8$) and male ($n = 13$) specimens was 178 cm and 186 cm, respectively (Cipriano 1992). Skulls from 41 animals had condylobasal lengths of 344–388 mm (Van Waerebeek 1993b).

Variation (geographic or other)—Based on regional morphological and genetic differences, differences in parasite load, and the

²⁷See note 11 above.

discontinuous distribution of *S. obscurus* across coastal and shelf waters of the Southern Hemisphere, four subspecies have been recognized by the Society for Marine Mammalogy's Committee on Taxonomy (2018):

1. *L. o. fitzroyi* (Waterhouse, 1838), "Fitzroy's dolphin" in Argentina.
2. *L. o. posidonia* (Philippi, 1893), "Peruvian/Chilean dusky dolphin" in Peru/Chile.
3. *L. o. obscurus* (Gray, 1828), "African dusky dolphin" in South Africa.
4. An unnamed subspecies, "New Zealand dusky dolphin" in New Zealand.²⁸

Color patterns associated with the four subspecies are shown in Würsig and Würsig (2010), although no significant variation has been found among the subspecies (Van Waerebeek 1993a).

Morphological studies have described significant differences among at least three of the subspecies (little has been published regarding morphological characteristics of specimens from Argentina; Van Waerebeek 1993a, b). Animals from Peru have larger total body lengths (~10 cm) and longer condylobasal lengths (~31 mm) compared to those from New Zealand and Africa (see *Meristics and osteology* above; Van Waerebeek 1993b). Crespo *et al.* (2007) noted that animals from Argentina are smaller (170 cm) than those from Peru and Chile (200 cm) but provided no further details. Animals from New Zealand have a smaller tooth size, higher tooth count, higher supraoccipital crest, wider external nares, and wider temporal fossa compared to those from Africa (Van Waerebeek 1993b). Some morphological differences have been documented between animals from Chile and Peru (*e.g.*, Chilean animals have lower tooth counts and shorter lower tooth row length), however, sample sizes from Chile are low ($n < 20$ for most measurements; Van Waerebeek 1993b).

Furthermore, there is support from both mitochondrial (*cyt-b* and mtCR) and nuclear DNA (nine microsatellites and Actin gene) data for the presence of four subspecies, as significant genetic differentiation has been found among the four geographic locations (Cassens *et al.* 2003, 2005; Harlin-Cognato *et al.* 2007).

Differences in breeding season are evident between Argentina (most births during summer; Würsig and Würsig 1980) and Peru (most births during winter) suggesting that these two subspecies are reproductively segregated (Van Waerebeek and Read 1994).

Parasitic roundworms (*Crassicauda* sp.) were documented in only one of 267 specimens from Peru and Chile (Van Waerebeek *et al.* 1993). However, although the sample size is small, *Crassicauda* was found in one of two specimens from South Africa (Van Waerebeek 1992). Whale lice (Cyamidae) were not observed on any *S. obscurus* specimens from Peru and Chile ($n = 267$; Van Waerebeek *et al.* 1993) but were found in two of 16 animals from New Zealand (Cipriano 1985).

²⁸The Society for Marine Mammalogy's Committee on Taxonomy (2018) has not accepted *L. obscurus superciliosus* as a subspecies for *L. obscurus* in New Zealand as proposed by Harlin-Cognato (2010).

Finally, there is some evidence for variation in seasonal movements among the subspecies. In Golfo San José, Argentina, abundance is low in winter and it peaks in summer, possibly related to the occurrence of main prey items (Würsig and Würsig 1980). In New Zealand, animals have been documented to occur in southern waters off of Kaikoura in summer months and to move into northern waters of the Marlborough Sound in winter months, likely in response to changes in water temperature (Gaskin 1968, Würsig *et al.* 1997, Harlin *et al.* 2003).

ACKNOWLEDGMENTS

This paper is one of the outcomes of the “Rethinking *Lagenorhynchus*” workshop held at the 2015 Biennial Meeting of the Society for Marine Mammalogy. The workshop was organized by EA and NLV and supported by a Special Event Award from the American Genetic Association (AGA). We sincerely thank all workshop participants for their contributions to discussions and their presentations. We also thank Anjanette Baker (AGA), Allison Galezo (Georgetown University), Al Gardner (United States Geological Survey), Tom Jefferson (Clymene Enterprises), Leslie Overstreet (Smithsonian Libraries), Barb Taylor (NOAA Southwest Fisheries Science Center), Marta Hevia (Fundación Cethus), and María Constanza Marchesi (CADIC-CONICET). Help with literature translations was provided by Amélia Viricel (Université de La Rochelle), Amy Driskel and Sergei Drovetski (Smithsonian Laboratories of Analytical Biology), Christian Ramp (Mingan Island Cetacean Study), Jose Zuniga (Global Genome Initiative), Lisa Schwartz (NOAA Southwest Fisheries Science Center), Mary Knight (American Museum of Natural History), Per Palsbøll (University of Groningen), Alison Flensburg, and Susan Mikuszewski. Research from Portugal was funded by the Portuguese Wildlife Society, SafeSea EEA-Grants, European Commission’s Life Programme (MarPro NAT/PT/00038). Finally, we thank all reviewers and editors who provided insightful and encouraging comments. This research was performed while NLV held an NRC Research Associateship award at NOAA Fisheries National Systematics Laboratory. The authors dedicate this publication to the memory of our friend and colleague, the late Rae Natalie Prosser de Goodall, whose contribution to understanding of *Lagenorhynchus* and *Cephalorhynchus* species in the southern cone of South America, especially around Tierra del Fuego, Argentina/Chile, is unparalleled.

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APPENDIX 1: NOMENCLATURAL NOTES

This appendix includes supplemental information, beyond that which is required for a species synonymy (see Gardner and Haysen 2004), for all of the species names included in the *Lagenorhynchus*, *Leucopleurus*, and *Sagmatias* synonymies. We provide this information to help decipher the complex nomenclatural histories for these species. Authorship notation is the same as previously described under Taxonomic Treatment and Species Descriptions.

LAGENORHYNCHUS ALBIROSTRIS GRAY, 1846

Delphinus Tursio: Brightwell, 1846:21, Plate 2

Not *Delphinus tursio* Fabricius, 1780. Unavailable name, misidentification. Description is given of animal “captured off Yarmouth” (Great Yarmouth, England). See Appendix 2 for more information.

Lagenorhynchus albirostris: Gray, 1846a:84

First use of current name combination. This is a reexamination of Brightwell’s skull. No type locality specified but is described as “North Sea, coast of Norfolk” (England) by Gray (1846b) and specified as “Yarmouth” (Gray 1850a).

Delphinus albirostris: Gray, 1846b:35, Plates 10 and 11

Name combination but was incorrectly used to refer to *Lagenorhynchus albirostris* (Gray 1846a).

Delphinus pseudotursio Reichenbach, 1846:Plate 24, Figure 76

Junior synonym. No type locality is specified. Drawing of external appearance is given with no other description. Figure legend reads “*Delphinus pseudotursio* Rchb. *Tursio* Th. *Brightwell. An. Mag. Nat. Hist. 1846.*” See “Nomenclatural Notes” in Galatius and Kinze (2016) for additional information.

Delphinus Ibsenii Eschricht, 1846:297

Junior synonym. No type locality specified but is stated as “N. Atlantic: Denmark” in Hershkovitz (1966) and “‘Agger Tange,’ West coast of Jutland, Denmark” in Galatius and Kinze (2016). Kinze (2018) states that Gray’s (1846*a*) description preceded that of Eschricht (1846) by eight months, thus making Gray’s *Lagenorhynchus albirostris* the senior synonym.

Delphinus (Lagenorhynchus) albirostris: Van Bénéden, 1860:28

Name combination. Provides description of external and internal morphological characteristics. States that the species inhabits “la mer du Nord (côtes d’Angleterre, de Danemark et de Belgique) et la Baltique (port de Kiel)” [North Sea (coasts of England, Denmark, Belgium) and the Baltic (port of Kiel, Germany)].

Refer to Galatius and Kinze (2016) for additional nomenclatural details and taxonomic history of *Lagenorhynchus albirostris* Gray, 1846.

LEUCOPLEURUS ACUTUS (GRAY, 1828)*Delphinus (Grampus) acutus* Gray, 1828:2

No type locality is specified. “Osse palatino carinato; rostro longo, attenuato, acuto, supra convexo, centro plano, longitudinaliter profunde sulcato; dentibus parvis, gracilibus, utrinque 28/28 – 30/30. Inhab. Cranium in Mus. D. Brookes. The length of the head is 7, that of the beak 8 inches; the breadth of the beak at its base $4\frac{1}{4}$.” According to Broekema (1983), the holotype of “*Grampus acutus* Gray, 1828. Skull. Brookes, 1828” is at the Rijksmuseum van Natuurlijke Historie, Leiden as specimen 18281.

Phocæna acutus: Gray in Brookes and Robins, 1828:39

Name combination. Appears in a catalog of items for sale by J. Brookes; specifically, “Cranium with teeth. Jaws of cranium with teeth” with no mention of species authority. Later referenced by Gray (1866*a*:270), as “*Phocæna acutus*, Gray, in Brookes’s Cat. Mus. 39, 1828” in a description for *Lagenorhynchus acutus*.

Delphinus Eschrichtii Schlegel, 1841:23, Plates 1 and 2 Figure 4, Plate 4 Figure 5

Junior synonym. Type locality is the “Fär-Inseln” (Faroe Islands). Schlegel notes the similarity with Gray’s (1828) *Delphinus acutus*. The holotype is in the “Leiden Museum” (Hershkovitz 1966). According to Broekema (1983), the holotype of “*Delphinus eschrichtii* Schlegel, 1841. Skeleton. ‘Iles Faër’. Eschricht, 1838” is at the Rijksmuseum van Natuurlijke Historie, Leiden as specimen 31210.

Delphinus leucopleurus Rasch, 1843:100, Plates 2 and 3

Junior synonym. No type locality specified. Hershkovitz (1966) states the type locality as the “Gulf of Christiania” (Norway) and “type skeleton in Christiania Museum.” Wiig and Bachmann (2013) provide additional information on the original description by Rasch, including information on the syntypes.

Lagenorhynchus leucopleurus: Gray, 1846b:34, Plate 6 Figures 3–5, Plate 12, Plate 26 Figure 3

Name combination, new name for *Delphinus leucopleurus* Rasch, 1843. Brief taxonomic description is provided. “Inhab. North Sea, Gulph of Christiania” (Norway), “[fetal] specimen and skeleton, Brit. Mus.” A more complete description of characters and taxonomy is given in Gray (1866a:273).

Lagenorhynchus acutus: Gray, 1846b:36

Name combination. Brief taxonomic description and measurements are provided. “Inhab. North Sea, Faroe Islands, *Eschricht*. Skulls and skeleton in the Leyden Museum.” The similarities to *D. leucopleurus*, per Professor Eschricht, are noted.

Electra acuta: Gray, 1868b:7

Name combination, new name for *Lagenorhynchus acutus*. Habitat is “North Sea.” Synonymized with *Leucopleurus arcticus* Gray, 1868 by Flower (1884).

Leucopleurus arcticus Gray, 1868b:7, Plate 6 Figures 3–5, Plate 12, Plate 26 Figure 3

Junior synonym, new name for *Lagenorhynchus leucopleurus* Gray, 1846. Type locality is “North Sea.” All plates are the same as in Gray (1846b) and labeled as *Lagenorhynchus leucopleurus* and not *Leucopleurus arcticus*. Synonymized with *Electra acuta* Gray, 1868 by Flower (1884). Hershkovitz (1966) incorrectly assigned “Gray, 1846” as the authority for *L. arcticus*.

Lagenorhynchus perspicillatus Cope, 1876:136, Plate 4

Junior synonym. Type locality is “near Portland, Maine” U.S.A. Description with measurements is given. The lectotype, designated as USNM 14244, is at the Smithsonian Institution’s National Museum of Natural History, Washington, D.C. (Fisher and Ludwig 2016). F. W. True, in a note not seen by us, indicated that Cope’s collection locality was not correct and “should be Woods Hole, Mass. or else Cape Cod” (Lyon and Osgood 1909, Fisher and Ludwig 2016).

Lagenorhynchus gubernator Cope, 1876:138

Junior synonym. Type locality is “near the same locality as the last” (near Portland, Maine, U.S.A.). Description with measurements is given. No holotype is known to exist, however a cast (USNM 12306) believed to represent the holotype is located at the Smithsonian Institution’s National Museum of Natural History, Washington, D.C. (Fisher and Ludwig 2016). F. W. True, in a note not seen by us, indicated that Cope’s collection locality is more specifically “from Casco

Bay, near Portland, Maine” (Lyon and Osgood 1909, Fisher and Ludwig 2016).

[*Lagenorhynchus*]. *bombifrons* Cope, 1876:138

Nomen nudum for *Lagenorhynchus gubernator*.

[*Lagenorhynchus*]. *acutus*: Flower, 1884:489, Figure 8

Name combination. Description provides information on the naming and taxonomic history of the genus and species.

Leicopleurus arcticus Tomilin, 1957:592

Incorrect subsequent spelling. According to Hershkovitz (1966), this is a “misprint listed in [Tomilin’s] synonymy of *Lagenorhynchus acutus* Gray, 1828.”

Leucopleurus acutus: LeDuc *et al.*, 1999:639, Figure 2

First use of current name combination. The new name is based on phylogenetic analyses of mitochondrial DNA data.

Delphinus leucoplaurus Wiig and Bachmann, 2013:595

Incorrect subsequent spelling of *Delphinus leucopleurus* Rasch, 1843 and listed in a discussion of the syntype specimen in the Natural History Museum, University of Oslo, Norway.

SAGMATIAS AUSTRALIS (PEALE, 1849)

Phocaena australis Peale, 1849:33

Type locality is “the South Atlantic Ocean, off the coast of Patagonia.” Short description and external measurements are given. The specimen was “Harpooned...on the 12th of February.” The specimen was to be printed on Plate 6 Figure 2 but the plates were not published in Peale’s volume (see Kellogg 1941). It is possible the skull and jaws used by Cope (1866) to describe *Sagmatias amblyodon* were originally part of Peale’s harpooned specimen; however, with the loss of some of Peale’s original notes and the lack/loss of associated collection history of Cope’s skull, whether these are two separate specimens or a single specimen will likely never be known (Kellogg 1941, Goodall *et al.* 1997c, Brownell *et al.* 1999a). Hershkovitz (1966) states that the type locality of *P. australis* is “...one day’s sail north of the Straits of Le Maire between Staten Island and Cape San Diego, Tierra del Fuego” (Argentina), however, this detail does not appear in either Peale (1849) or Cassin (1858; a republication of Peale 1849) but was included in Kellogg’s (1941:296) type description.

Delphinus obscurus (in part): Cassin, 1858:27, Plate 5 Figure 1

Name combination. Cassin, in his republication of Peale (1849) and using mostly Peale’s original description, synonymized *Phocaena australis* with *Delphinus obscurus* Gray, 1828 (Kellogg 1941, Goodall *et al.* 1997c).

Sagmatias amblyodon Cope, 1866:294

No type locality specified. Junior synonym. Description and measurements of the holotype (skull only) is provided. The type

information is described under the Taxonomic Treatment of *Sagmatias* and *S. australis*. Also, see note above under “*Phocaena australis* Peale, 1849” about the collection history of *S. amblodon* and *Phocaena australis*.

Delphinus chilensis Philippi, 1895:283

Unavailable name, misidentification. Brief description of the specimen (fetus) is given. Philippi (1896:10, Plate 2 Figure 3) provides an external description and measurements. The current authors believe that the identification of Mead and Brownell (2005:729) is in error and the fetus is not identified as a synonym of *Lagenorhynchus australis*, but rather it should be defined as “Delphinid sp.” See Appendix 2 for more information.

Tursio chiloensis Philippi, 1900:10, unlabeled illustration

Junior synonym. Type locality is “no mui distante de Ancud” (translated as: not very far from Ancud [Chile]). Description and measurements of a partial skull found near Ancud, Chile (on Chiloé Island; also see Philippi 1901). Determined by Goodall (1986) to be *Lagenorhynchus australis*. The partial skull is housed at the Museo Nacional de Historia Natural in Santiago, Chile as specimen MNHN-S 586 (formerly 583; Goodall 1986).

Lagenorhynchus australis: Kellogg, 1941:296

Name combination. Synonymy and taxonomic description are given. Concerning the holotype, it is stated that “Nothing is known about this specimen. Off coast of Patagonia, one day’s sail north of the Straits of Le Maire between Staten Island and Cape San Diego, Tierra del Fuego. Collected February 12, 1839, by someone on one of the ships of the United States Exploring Expedition, 1838–1842.”

Lagenorhynchus cruciger (in part): Bierman and Slijper, 1947:1362

Name combination. Based on similarities in distribution, total body length, tooth count, vertebral count, skull shape, and external appearance, *L. australis* was considered to be the same species as *L. cruciger*.

Sagmatias. *australis*: LeDuc *et al.*, 1999:636, Figure 2

First use of current name combination. The new name is based on phylogenetic analyses of mitochondrial DNA data.

Sagmatias australis: Moreno, 2008:23, Table 2

Name combination. This name appears in a Delphinidae classification modified from LeDuc (2002). Moreno’s use of this name is a modification of how it initially appeared in LeDuc *et al.* (1999).

Cephalorhynchus australis: Moreno, 2008:79

Name combination. Based on analysis of morphological characters. Synonymy and diagnostic description are given.

Refer to Kellogg (1941) and Goodall *et al.* (1997c) for additional nomenclatural details and taxonomic history of *Sagmatias australis* (Peale, 1849).

SAGMATIAS CRUCIGER (QUOY AND GAIMARD, 1824)

Delphinus cruciger Quoy and Gaimard, 1824:87, Plate 11 Figures 3 and 4

Type locality is between “Nouvelle-Hollande et le cap Horn” (New Holland [Australia] and Cape Horn [Chile]) in January of 1820 around 49°S. Drawings of lateral and dorsal views are given, along with a description of the external appearance: “...d’autres dauphins ayant de chaque côté du corps, dans presque toute sa longueur, deux larges lignes blanches, coupées à angle droit par une noire; ce qui, vu par le dos, formoit une croix noire sur un fond blanc” (translated as: dolphins with two broad white lines on each side of the body that seemed to make a black cross on a white background when seen from above). No specimens of these dolphins were taken on this voyage. A specimen was collected by d’Orbigny and Gervais (1847:32, Plate 21 Figures 1–4) between 57°S and 76°S²⁹ (southeast of Cape Horn). Note that in d’Orbigny and Gervais (1847) the plate number is incorrectly written as “XXIII.” The skull was deposited in the “Muséum d’histoire naturelle” in Paris, and according to Goodall *et al.* (1997a) the skull was subsequently “labeled *D. bivittatus* (see photograph in Robineau, 1990) and given the number A.3045.” d’Orbigny and Gervais (1847) synonymized their specimen with *D. cruciger* Quoy and Gaimard, 1824, *D. bivittatus* Lesson in Lesson and Garnot, 1827, and both *D. cruciger* and *D. bivittatus* “*livitatus*” of Cuvier (1836).

Delphinus albigena Quoy and Gaimard, 1824:87, Plate 11 Figure 2

Junior synonym. Type locality is close to New Holland (Australia) and Cape Horn, Chile as this specimen was collected “quelques jours après” (translated as: a few days after) *Delphinus cruciger* Quoy and Gaimard, 1824. Dolphins were seen on the same voyage and a few days after those distinguished as *D. cruciger* (above), therefore presumably also observed between Australia and Chile, around 49°S in January of 1820. A lateral drawing and a short description of external appearance are given: “...et qui se faisoit remarquer par une bandelette blanche de chaque côté de la tête” (translated as: having a white strip on each side of the head). Quoy and Gaimard also noted that *D. albigena* might be a younger form of *D. cruciger*.

Delphinus bivittatus Lesson in Lesson and Garnot, 1827:178, Plate 9 Figure 3 (Atlas)

Junior synonym. Type locality is “Dans les mers orageuses du cap Horn, en allant aux Malouines, à cent quarante lieues de ces îles” (translated as: In the stormy seas of Cape Horn, on the way to the Falklands, a hundred and forty leagues from these islands). A description of the animal in the water is given noting on the sides of the body a broad white band interrupted by a line of black below the dorsal fin. Lesson notes the similarity to *D. cruciger* Quoy and

²⁹According to Philippi (1893), the location of 76°S was an error, stating that the ship never went that far south. Goodall (1997) suggests it is a misprint of 66°S.

Gaimard, 1824, but designated a new name based on differences in color pattern in comparison to Quoy and Gaimard's drawing.

Phocaena Homeii Smith, 1829:440

Junior synonym. Type locality is "the seas about the Cape of Good Hope." Description of external characteristics of a black and white dolphin that is found around "the Cape of Good Hope, and is often caught in Table Bay" (South Africa). According to Hershkovitz (1966), "type in the South African Museum."

Delphinus livitatus F. Cuvier, 1836:225

Incorrect subsequent spelling. A misspelling of *Delphinus bivittatus* Lesson in Lesson and Garnot, 1827. According to Hershkovitz (1966), "regarded as not certainly identifiable."

D[elphinus]. albigenus: Gray, 1846b:44

Justified emendation, correction of gender agreement. Several species, including "*D. cruciger*, Quoy & Gaim.", "*D. bivittatus*, Lesson", and "*D. albigenus*, Quoy", are listed as species that "...have been named and figured by the sight caught of them when swimming!" The reference to *D. albigenus* includes "*l.c.t.11, f. 2*" which matches the plate and figure numbers from *Delphinus albigena* Quoy and Gaimard, 1824.

Lagenorhynchus clanculus Gray, 1846b:Plate 35

Junior synonym. No type locality specified. There is no text or description, only a drawing of the skull labeled with the name. Gray (1849, 1850b) gives a description and provides measurements of the skull and states that the specimen was collected by Dr. Dickie, transferred to the British Museum, and type location is listed as "Pacific." Additional information on the specimen is provided in Gray (1850a, 1866a), including specific reference to the drawing from Gray (1846b:Plate 35) and notes that the skull is from the "Pacific Ocean" and "Dr. Dickie's Collection." Flower (1885:23) states that the holotype (skull) was collected in the Pacific Ocean, is in the British Museum (no. 935 a-49.5.25.3), and was purchased from Dr. Dickie's Collection in 1849. According to Brownell and Donahue (1999), the British Museum specimen is labeled "No. 1849.5.25.3-935a." According to the British Museum (Natural History), London online catalog (accessed July 25, 2017), the holotype (skull) with locality "Pacific" is no. 1849.5.25.3. Fraser and Noble (1968) show Gray's (1846b) *L. clanculus* specimen has similar cranial morphological characteristics compared to *L. cruciger* and is substantially different from *L. australis*.

D[elphinus]. bivittatus: Gay, 1847:175

Name combination. This is a reference to *D. bivittatus* Lesson in Lesson and Garnot, 1827 and it provides a brief external description of the species as seen around Cape Horn, Chile.

D[elphinus]. cruciger: Gay, 1847:175

Name combination. This is a reference to *D. cruciger* Quoy and Gaimard, 1824 and it provides a brief external description of the

species as seen around Cape Horn, Chile and mentions that this species appears to be the same as *D. bivittatus*.

Delphinus obscurus: Gray, 1850a:107

Name combination. Synonymizes *D. cruciger* Quoy and Gaimard, 1824, *D. bivittatus* Lesson in Lesson and Garnot, 1827, and *D. albigena* Quoy and Gaimard, 1824, among others. Gray states that “there is a skull named *D. bivittatus*, D’Orbigny 1830, in the Paris Museum” and presumes that this skull is that of the specimen figured and labeled as “*D. cruciger*, D’Orb. Voy. Amér. Mérid. Mam. t. 21.” This name is incorrectly cited as “*Lagenorhynchus obscurus* Gray 1850b” in Goodall *et al.*’s (1997a) synonymy.

Electra clancula: Gray, 1868b:7, Plate 35

Name combination. New name for *Lagenorhynchus clanculus* Gray, 1846. The plates in both publications depict the same drawing (e.g., description based on the same skull, both labeled “*Lagenorhynchus clanculus*”). The entire description is given as “*Lagenorhynchus clanculus*, Gray, l. c. 271, 272, 275. Beak af [sic] the skull broad behind, once and three-fourths the width of the notch in length. Teeth five in an inch. Hab. South Pacific Ocean.”

Electra crucigera: Gray, 1871:77

Name combination. New name for “*Lagenorhynchus cruciger*, Gervais, Ostéogr. Cét. tab. 36. fig 3” (Van Bénédén and Gervais 1880). Note that Hershkovitz (1966:63) incorrectly names “*Electra crucigera*, Gray, 1870.” The correct name for that reference is *Electra clancula* Gray, 1870:393.

Lagenorhynchus cruciger: Van Bénédén and Gervais, 1880:598, Plate 36 Figure 3

Name combination. The text incorrectly says “Pl. XXXXVI, fig. 3.” Synonymized with *Delphinus cruciger* Quoy and Gaimard, 1824, *D. bivittatus* Lesson in Lesson and Garnot, 1827, *D. cruciger* and *D. bivittatus* “*livitatus*” (Cuvier 1836), and *D. cruciger* (d’Orbigny and Gervais 1847). The works of Van Bénédén and Gervais were published throughout the period 1868–1880, therefore the name “*Lagenorhynchus cruciger*” was attributed to one or both authors during dates/publications prior to 1880 (e.g., see *Electra crucigera* Gray, 1871:77). Later, Bierman and Slijper (1947) synonymized “all southern species of *Lagenorhynchus*” including *L. obscurus* (Gray, 1828), *L. fitzroyi* (Waterhouse, 1838), *L. wilsoni* Lillie, 1915, *L. australis* (Peale, 1849), and *L. superciliosus* (Lesson in Lesson and Garnot, 1827) with *L. cruciger* (Quoy and Gaimard, 1824).

Lagenorhynchus latifrons True, 1889:84, 90

Junior synonym. No type locality specified. No authority or year is given, but the use of the name includes notes of “Paris Museum” and “Paris Museum, No. a3041, labeled *L. latifrons*, New Zealand” (p. 84 and 90, respectively). Listed as a synonym of “*Lagenorhynchus cruciger* d’Orbigny and Gervais. 1847” and “*Lagenorhynchus clanculus*, Gray. 1849.” Goodall *et al.* (1997a) states “Label

on skull MNHN-P a3041 from New Zealand, listed by True (1889) but not described in the literature”, and in Hershkovitz (1966): “ms. name in synonymy of *L. cruciger* based on skull, Paris Museum, no. a3041, from New Zealand.”

Phocaena d'Orbignyi Philippi, 1893:10, Plate 2 Figure 2 (“*Phocaena D'Orbignyi* Ph.”)

Junior synonym. No type locality specified. The figure is reproduced from the original publication of d'Orbigny and Gervais (1847). Based on differences in external appearance, Philippi was convinced d'Orbigny and Gervais's (1847) animal was not *Delphinus cruciger* and thus provided a new name.

Phocaena crucigera: Philippi, 1893:11, Plate 3 Figure 4 (“*Ph. bivittata* Lesson”) and Figure 5 (“*Ph. crucigera* Quoy et Gaim.”)

Name combination. Both figures are reproduced from the original publications of Lesson and Garnot (1827) and Quoy and Gaimard (1824). Synonymizing *Delphinus bivittatus* Lesson in Lesson and Garnot, 1827 and *Delphinus cruciger* Quoy and Gaimard, 1824 under a new name.

Tursio obscurus: Gray, 1866a (Philippi 1896):17

Name combination. Philippi (1896) synonymizes *Delphinus cruciger* Quoy and Gaimard, 1824, “*D. bivittatus* d'Orb. Voy. Am. etc., tab. XXI” (d'Orbigny and Gervais 1847; see note above about skull for *Delphinus obscurus* Gray, 1850a), and *D. Fitzroyi* Waterhouse, 1838 with Gray's (1866a:264) *Tursio obscurus*. The synonymy of Goodall *et al.* (1997a) gives the authority as “*Tursio obscurus* Gray-Philippi, 1896.”

Lagenorhynchus Fitzroyi: Lahille, 1899:200

Unavailable name, misidentification. A brief mention of the species is given: “*Lagenorhynchus Fitzroyi* (Waterhouse) Bahía San Matías-Muy común.” Hershkovitz (1966:66) mistakenly cites “Lahille, 1892” and page 36 for this name. Liouville (1913:165, Figure 17 (p. 172), Plates 8 and 9) provides a thorough review of naming history, a description of external and internal characteristics and known distribution, and synonymizes previously described *Lagenorhynchus/Delphinus/Phocaena* specimens of *cruciger*, *bivittatus*, *Fitzroyi*, and *clanculus*. See Appendix 2 for more information.

Lagenorhynchus wilsoni Lillie, 1915:123

Junior synonym. No type locality specified, but it “would seem to be confined to a comparatively narrow band of the Southern Ocean, just north of the pack-ice, between Lat. 65° S. and Lat. 54° S.” A description of an “undescribed Dolphin” seen from the *Discovery* by Dr. E. A. Wilson between 1901 and 1904 (Wilson 1907:9, Figure 7). Wilson (1907) saw the dolphin “in abundance in the outer zone of the Antarctic pack ice...on November 19th in about the same latitude in which we had seen *Lagenorhynchus obscurus* [between 55° and 60°S lat. in 135°E. long] but farther to the east.” No specimen was taken and the description is based off of seeing the animal

swimming in the water. Lillie also notes that it is possible this is the same type of dolphin as *L. fitzroyi* (Liouville, 1913). "*L. wilsoni*" is mentioned as being "Nearly allied to if specifically distinguishable" from *L. cruciger* (Quoy and Gaimard, 1824) (Norman and Fraser 1937, Hershkovitz 1966).

[Lagenorhynchus]. cruciger: Yañez, 1948:115

Name combination. This is a reference to *L. cruciger* (Quoy and Gaimard, 1824). It provides a brief external description of the species as seen around Cape Horn and Tierra del Fuego (Chile/Argentina).

Sagmatias cruciger: LeDuc *et al.*, 1999:636, Figure 2

First use of current name combination. The new name is based on phylogenetic analyses of mitochondrial DNA data.

Cephalorhynchus cruciger: Moreno, 2008:79

Name combination. New name based on analysis of morphological characters. Synonymy and diagnostic description are given; however, note that Moreno (2008) did not include morphological data from *cruciger* and states that "In this study [it] was not possible to examine a complete skull of *C. cruciger* but, it is the sister species of *C. australis* as pointed out by the recent molecular phylogenies...."

Refer to Goodall *et al.* (1997a) and Brownell and Donahue (1999) for additional nomenclatural details and taxonomic history of *Sagmatias cruciger* (Quoy and Gaimard, 1824).

SAGMATIAS OBLIQUIDENS (GILL, 1865)

Lagenorhynchus obliquidens Gill, 1865:177

Name combination. Type locality is "San Francisco, California." A description of skull characteristics is provided and states that "three skulls of adults of this species, obtained at San Francisco, California, are in the Smithsonian collection." These skulls exist as syntypes (USNM 1961, 1962, and 1963) at the Smithsonian Institution's National Museum of Natural History, Washington, D.C. (Fisher and Ludwig 2016).

Delphinus longidens Cope, 1866:295

Junior synonym. No type locality specified. A description and some measurements of the skull are provided and states "Habitat unknown. Museum Smithsonian, No. 3886." The holotype exists as a skull (USNM 3886, type locality "unknown") at the Smithsonian Institution's National Museum of Natural History, Washington, D.C. (Fisher and Ludwig 2016).

Clymenia similis Gray, 1868b:6

Unavailable name, misidentification (based on habitat of Cape of Good Hope). "Skull like *C. obscura*, but palate contracted behind; side of pterygoid bone keeled. *Hab.* Cape of Good Hope." True (1889:99–100) states that for *C. similis* the "skull on which this

species is founded can not be distinguished from skulls of *L. obliquidens*”, and it “agrees in many points with *L. obscurus*...and it is not at all impossible that the skulls now distributed among the three species, *obscurus*, *obliquidens*, and *similis*, represent only the individual variations of a single species.” See Appendix 2 for more information.

Lagenorhynchus longidens: True, 1889:99

Name combination. New name for *Delphinus longidens* Cope, 1866 after reexamination of the holotype skull. True also states that “After repeatedly examining the skull, I have become convinced that it is simply a small and youngish example of *L. obliquidens*.”

Lagenorhynchus ognevi Sleptsov, 1955:60, Figures 1–3

Junior synonym. Type locality is “in the Nemoro Sea, 15–20 miles east of the South Kuril Cape (Kunashir Island).” A thorough taxonomic description, including external and internal measurements, of four specimens collected from southeastern Russia (Kunashir Island, Amur Bay, Vityaz Bay) between 1951 and 1954 is given. Numerous morphological differences were highlighted by Sleptsov to justify designating these specimens as belonging to a different species compared to *L. obliquidens*. All four specimens, designated as syntypes, were given to the Zoological Museum of Moscow University.

(*S[agmatias]*.) *obliquidens*: LeDuc et al., 1999:639, Figure 2

First use of current name combination. The new name is based on phylogenetic analyses of mitochondrial DNA data.

Sagmatias obliquidens: Moreno, 2008:23, Table 2

Name Combination. This name appears in a Delphinidae classification modified from LeDuc (2002). Moreno’s use of this name is a modification of how it initially appeared in LeDuc et al. (1999).

SAGMATIAS OBSCURUS (GRAY, 1828)

Delphinus superciliosus Lesson in Lesson and Garnot, 1827:181, Plate 9 Figure 2 (Atlas)

Nomen dubium. A brief description of a harpooned animal observed at 44°S by Cape Diemen (south Tasmania) is given; however, a specimen was not preserved (or perhaps was lost or discarded); a drawing was made of the lateral external appearance. Schlegel (1841:22, Plate 1 Figure 3, Plate 2 Figure 3, Plate 4 Figure 4) describes a skeleton from an animal collected by the Cape of Good Hope, South Africa that was sent by van Horstock to the “Leyden Museum” and identified as *D. superciliosus* (True 1889). Lesson’s specimen was not preserved and the exact collection location is unknown, therefore the identity of this animal cannot be confirmed and is possibly either *obscurus* or *cruciger* (also see Meester et al. 1986:157). Because Lesson’s specimen is unidentifiable, and to promote stability of taxonomic nomenclature (Article 23.2 ICZN 1999, Melville 1995), the species name *superciliosus* should not

have priority over that of *D. obscurus* Gray, 1828. Both Hershkovitz (1966:64) and Rice (1998:115) include *Delphinus superciliosus* Lesson in Lesson and Garnot, 1827 as a synonym of *Lagenorhynchus cruciger*, but we believe this nominal species should be treated as a *nomen dubium*. Also, note that the collection location “Castle-Forbes” (Hershkovitz 1966:64) is the name of an English vessel and not a place.

Phocoena superciliosa: Lesson, 1827:415

Name combination. New name for *Delphinus superciliosus* Lesson in Lesson and Garnot, 1827. A short description is provided, the habitat is “les mers antarctiques” (the Antarctic seas).

Delphinus (Grampus) obscurus Gray, 1828:2, Plate 2 Figures 2–5

Type locality is “Cape of Good Hope” (South Africa) and the specimen is in the “Mus. Coll. of Surgeons.” External descriptions of animals from various life stages are given. According to Hershkovitz (1966), “stuffed skins of adults and young with skull inside, originally in the Royal College of Surgeons, London; adult with skull removed now in British Museum, no. 41.1733 (cf. Flower, 1885, List Cetacea Brit. Mus., pg. 28).” According to the British Museum (Natural History), London online database, this specimen is catalog no. 1841.1733 (accessed 21 July 2017).

Delphinus obscurus (variété): Quoy and Gaimard, 1830:151, Plate 28 Figure 2

Junior synonym. Type locality is “le cap de Bonne-Espérance” (Cape of Good Hope), South Africa. The specimen is believed to be a variety of *D. obscurus* Gray, 1828 and differing in color pattern. A brief external description is given with some measurements. A prepared specimen is in the Natural History Museum of Cape Town (Iziko South African Museum), South Africa. The current authors have not seen the original plate/figure from Quoy and Gaimard (1830), but the image was reproduced by Kellogg (1941) in Plate 7 Figure 2.

Delphinus Fitzroyi Waterhouse, 1838:23

Junior synonym. Type locality is “in the Bay of St. Joseph” and “coast of Patagonia, Lat. 42°30’” (Argentina). External measurements and description are given and the similarity to *D. superciliosus* Lesson in Lesson and Garnot, 1827 is noted. Waterhouse (1839:25, Plate 10) provides further details including that the specimen was harpooned “in the Bay of St. Joseph” and the habitat is “coast of Patagonia, Lat. 42°30’, (April).” According to Hershkovitz (1966), “type a female, rostrum and anterior portion of lower jaw, in British Museum, collected by Charles Darwin.” According to the British Museum (Natural History), London online database, this specimen is catalog no. 1939.2.18.1 with a locality of “Bay of St. Joseph, coast of Patagonia” (Argentina; accessed 18 July 2017).

Delphinus breviceps Wagner, 1846:427, Plate 368 Figure 1

Junior synonym. No type locality specified but is stated as “Rio de la Plata” (Argentina) by Jacquinot and Pucheran (1853). The scientific

name is listed in the appendix and a drawing of the animal is provided. Jacquinot and Pucheran (1853:39) and Jacquinot (1842–1853; Plate 22 Figure 1, Plate 23 Figures 5 and 6) reference Wagner's drawing as "Dauphin a [with accent grave] museau court. – *Delphinus breviceps*." Gray (1846*b*) states that "The skull, *Dauphin à museau court*" is "in the Paris Museum." Kellogg (1941) states that *D. breviceps* should be regarded as a color variant of "the porpoise hitherto known as *Lagenorhynchus fitzroyi*." Robineau (1990), after reexamining the specimen, considered it to be a synonym of *L. obscurus*. Therefore, the holotype exists as a skeleton of a specimen collected from Rio de la Plata (Argentina) "à 20 lieues de l'embouchure" [about 20 leagues from the mouth] on the expedition of the *Astrolabe* and the *Zélée* commanded by Dumont d'Urville, serial no. JAC:1880-646 at the Laboratory of Comparative Anatomy of the National Museum of Natural History (Paris; Robineau 1990). See True (1889), Kellogg (1941), Robineau (1990), and Brownell and Cipriano (1999) for more information on the history of this specimen.

Delphinus obscurus: Gray, 1846*b*:37, Plate 16

Name combination. A brief description is given and Gray synonymizes the previous names listed above. It inhabits the "Southern Ocean, Cape *Heaviside*."

Lagenorhynchus? nilssonii Gray, 1864:238

Unavailable name, misidentification. Name for a specimen "Nilsson, in the 'Scandinavian Fauna,' records...under the name *Delphinus obscurus*, and refers it with doubt to the description and figure of the skull, and the species under that name, in the 'Zoology of the Erebus and Terror,' and equally with doubt to *D. superciliosus* of Schlegel." Gray states that Nilsson's species "may very likely be found in the British Seas." According to Lilljeborg (1866:231), Nilsson's skull is from an unknown location and is preserved in the "Museum of Lund." Malm (1871:60) states that the skull was delivered to the "Lund, Universitets zool. Museum" by Professor Florman and notes doubt that the specimen was taken from the Swedish coast. Upon further examination of the skull, Malm (1871:60) determined that it belonged to *Chymenia doris* Gray, 1868 (= *Stenella frontalis* G. Cuvier, 1829). See Appendix 2 for more information.

Tursio obscurus: Gray, 1866*a*:264

Name combination. Provides brief description and synonymizes many names that are now known to represent *Sagmatias cruciger*, *S. obscurus*, and *S. australis*. Inhabits "Southern Ocean, Cape (*Heaviside*)."

Lagenorhynchus breviceps: Gray, 1866*a*:271

Name combination. New name for *Delphinus breviceps* Wagner, 1846. A brief description is provided and it inhabits "Rio de la Plata" (Argentina).

Clymene obscura: Gray, 1866*b*:215

Name combination. New name for *Tursio obscurus* Gray, 1866. A brief description is provided.

D[elphinus]. (Tursio) obscurus: Cope, 1866:295

Name combination. The name is mentioned in a description of a *D. longidens* skull.

Delphinus (Tursio) obscurus: Burmeister, 1867:306

Name combination. Synonymizes *Delphinus obscurus* (Gray 1828, 1846b, 1866a), *D. fitzroyi* Waterhouse, 1838, and *D. bivittatus* (d'Orbigny and Gervais 1847).

Clymene similis Gray, 1868a:146, Figure 2

Junior synonym. Type locality is "Cape of Good Hope (*Layard*)" (South Africa). This species is differentiated from *Clymene obscura* Gray, 1866 based on differences in tooth size and shape of the palate and pterygoid bones (the latter is drawn in Figure 2). The holotype specimen (skull) is in "the British Museum, no. 1509b" (Hershkovitz 1966; British Museum (Natural History), London online database, accessed July 26, 2017).

Clymenia obscura Gray, 1868b:6, Plate 16

Unjustified emendation. Synonymizes *Delphinus obscurus* (Gray, 1846), *Tursio obscurus* Gray, 1866, and *Clymene obscura* Gray, 1866. A brief description is provided and the habitat is "South Pacific." Note that Plate 16 is labeled as "*Delphinus obscurus*."

Clymenia similis Gray, 1868b:6

Unjustified emendation. "Skull like *C. obscura*, but palate contracted behind; side of pterygoid bone keeled. *Hab.* Cape of Good Hope" (South Africa).

[lymenia]. obscura: Gray, 1870:393, 394

Name combination. Name listed under species that have been found in the waters of "South America" and "South Africa" (p. 393 and 394, respectively).

Electra breviceps: Gray, 1871:76

Name combination. "*Lagenorhynchus breviceps*, Gervais, Ostéog. Cét. tab. 36. fig. 3. Inhab. - ?." The online World Register of Marine Species database (accessed 24 July 2017) lists "*Electra breviceps* Gray, 1868" as a synonym of *L. obscurus*, however the current authors were unable to verify the use of the name any earlier than Gray (1871).

Lagenorhynchus fitzroyi: Flower, 1885:23

Name combination. New name for *Delphinus fitzroyi* Waterhouse, 1838. A brief description of the holotype specimen is provided. The type locality is "Bay of St. Joseph, coast of Patagonia, lat. 42°30', April."

Prodelphinus obscurus: Flower, 1885:28

Name combination. New name for *Delphinus obscurus* Gray, 1828. A history of known specimens of this species, including the holotype, in the British Museum is provided.

Prodelphinus superciliosus: Jentink, 1887:173

Name combination. No type locality specified. New name for *Prodelphinus obscurus* Flower, 1885. Jentink documents that the

skeleton collected by Captain De M. von Horstock and pictured in Schlegel (1841:22, Plate 1 Figure 3, Plate 2 Figure 3, Plate 4 Figure 4) is in the collections of the "Musée d'Histoire Naturelle des Pays-Bas" (the Natural History Museum of the Netherlands). According to Broekema (1983), the holotype of "*Prodelphinus superciliosus* Garnot et Lesson *a*. Skeleton, mounted. Cape, South Africa. Van Horstock, 1825–1835" is at the Rijksmuseum van Natuurlijke Historie, Leiden as specimen 24764. In Broekema (1983), this holotype is listed under "*Lagenorhynchus cruciger* (Quoy & Gaimard, 1824)."

Prodelphinus Petersii Lütken, 1889:43

Junior synonym. Description, measurements (p. 41), and drawing (skull p. 43) of a dolphin collected from "Øen Amsterdam i det indiske Hav" [The island of Amsterdam in the Indian Ocean] are provided. The holotype specimen was examined and confirmed as *Lagenorhynchus obscurus* by Van Waerebeek *et al.* (1995). The holotype exists as a mounted skeleton collected "near Amsterdam Island (37°55'S, 77°40'E) in the Southern Indian Ocean by S. Hiits" and is stored at the Zoological Museum, Copenhagen as specimen UZMC-5 (Van Waerebeek *et al.* 1995). Hershkovitz (1966:30) lists *P. Petersii* as a synonym of *Stenella coeruleoalba*, however this was determined as incorrect by Van Waerebeek *et al.* (1995).

Lagenorhynchus superciliosus: True, 1889:92, Plate 25 Figure 3

Name combination. New name for *Delphinus superciliosus* (Schlegel, 1841). Taxonomic history and measurements are provided of Van Horstock's skeleton "sent to the Leyden Museum...from the Cape of Good Hope" (South Africa).

Lagenorhynchus obscurus: True, 1889:104, Plate 29 Figures 1 and 2

Name combination. Synonymizes *Delphinus obscurus* Gray, 1828, *Tursio obscurus* Gray, 1866, *Clymenia obscura* (Gray 1866*b*), and "? *Phocaena australis*" (Peale 1849). A brief taxonomic history and table of measurements is provided.

Lagenorhynchus obscurum Blanford, 1891:580

Junior synonym. Type locality is "Palk Straits, Ceylon" (Sri Lanka). New name for *Delphinus obscurus* Gray, 1828. A brief description and a few measurements are provided. The color description appears to be taken from Gray (1828) and the type is a skull "in the Museum, Calcutta." Note that the location (Sri Lanka) is currently not considered part of the range of *S. obscurus*, therefore the identity of this specimen needs to be verified. Hershkovitz (1966:70) includes *L. obscurum* in the synonymy of *Lagenorhynchus electra* (= *Peponocephala electra*).

Phocaena posidonia Philippi, 1893:9, Plate 2 Figure 1

Junior synonym. Type locality is "48°10' latit. sur i 77° lonjit. oeste" (48°10' latitude south and 77° longitude west) in Chile. Measurements and external description are given. A female specimen was harpooned. Similarities with *Delphinus Fitzroyi* Waterhouse, 1838 are noted but a new name was given based on differences in head

shape and coloration. According to Hershkovitz (1966), the holotype exists as a skin and skull of a female collected off the coast of Chile (48°10'S and 77°W) and stored in the "Santiago de Chile Museum." Brownell and Cipriano (1999) concluded that *P. posidonia* is a junior synonym of *Lagenorhynchus obscurus*.

Phocaena fitzroyi: Philippi, 1893:13, Plate 5 Figure 2

Name combination. New name for *Delphinus Fitzroyi* Waterhouse, 1838. Measurements and external description are given. The habitat is the coast of Patagonia, 42°30'S latitude. Philippi also notes the similarities to both *Delphinus superciliosus* Lesson in Lesson and Garnot, 1827 and *P. posidonia* Philippi, 1893.

Tursio? Panope Philippi, 1895:284

Junior synonym. No type locality specified. A brief description is given. Philippi (1896:14, Plate 4 Figure 2, Plate 5 Figure 2, Plate 6 Figure 2) further describes the skull and provides some measurements. The skull, catalog number MNHN 584, is from the Museo Nacional de Historia Natural, Santiago, Chile (Brownell and Cipriano 1999, Canto 2014). True (1903) proposed this specimen belonged to a genus "not hitherto known", however Brownell and Mead (1989) examined the skull and verified it was a specimen of *Lagenorhynchus obscurus* (Gray 1828), a finding that was later confirmed by Canto (2014).

Lagenorhynchus thicola breviceps: Trouessart, 1898–1899:1038

Name combination. Synonymized *Delphinus breviceps* (Jacquinot 1842–1853) and others.

Lagenorhynchus Fitzroyi: Lahille, 1899:200

Name combination. A brief mention of species is given: "*Lagenorhynchus Fitzroyi* (Waterhouse) Bahía San Matías - Muy común." Hershkovitz (1966:66) mistakenly cites "Lahille, 1892" and p. 36 for this name.

[*Lagenorhynchus*]. *posidonia*: True, 1903:137, 138

Name combination. New name for *Phocaena posidonia* Philippi, 1893. True determined that based on the shape of the head from Plate 2 Figure 1 (Philippi 1893) the species should be assigned to *Lagenorhynchus* and not *Phocaena* and, based on color differences, should be a separate species compared to *Lagenorhynchus fitzroyi* Waterhouse, 1838.

Lissodelphis ? panope: Trouessart, 1904:766

Name combination. New name for *Tursio? Panope* (Philippi 1896, True 1903).

Lagenorhynchus superciliosus Trouessart, 1904:767

Incorrect subsequent spelling. Misspelling of *Lagenorhynchus superciliosus* Lesson in Lesson and Garnot, 1827.

[*Lagenorhynchus*]. *obscurus*: Schneider, 1946:80

Name combination. "*L. obscurus*, Gray. Tunina negra. Es la especie más frecuente en el litoral, abundando en el Golfo de Arauco y en

los alrededores de la desembocadura del río Bío-Bío.” (translated as: Black porpoise. It is the most frequent species in the coast [of Chile], abounding in the Gulf of Arauco and in the surroundings of the mouth of the Bío-Bío River).

Lagenorhynchus fitzroyi Bini, 1951:91, Figures 12 and 13

Incorrect subsequent spelling. Misspelling of *Lagenorhynchus fitzroyi*. Animal seen in May of 1949 about three miles from the northern coast of Atico, Peru.

(*Sagmatias*) *obscurus*: LeDuc *et al.*, 1999:639, Figure 2

First use of current name combination. The new name is based on phylogenetic analyses of mitochondrial DNA data.

Sagmatias obscurus: Mann *et al.*, 2002:348, Appendix 2

Name Combination. This name appears in a “Systematic revision of delphinidae” and is modified from LeDuc *et al.* (1999).

APPENDIX 2: MISIDENTIFICATIONS

The following are species that are either found within a *Lagenorhynchus* synonymy and were subsequently determined to be a misidentification (*i.e.*, determined to be a different genus and/or species), or were initially named *Lagenorhynchus* but were determined to be a misidentification and therefore appear in the synonymy of other genera (*e.g.*, *Cephalorhynchus*) and not that of *Lagenorhynchus*.

Misidentifications Found Within Lagenorhynchus Synonymies

Delphinus Tursio: Brightwell, 1846:21, Plate 2. Not *Delphinus tursio* Fabricius, 1780. Considered *incertae sedis* by Hershkovitz (1966:199). Appears in *Lagenorhynchus albirostris* synonymy.

Lagenorhynchus? nilssonii Gray, 1864:238. Appears in *Sagmatias obscurus* synonymy but was identified by Malm (1871) as *Clymenia doris* Gray, 1868 (= *Stenella frontalis* G. Cuvier, 1829).

Clymenia similis Gray, 1868b:6. Appears in the synonymies of both *Sagmatias obliquidens* and *S. obscurus*. Based on the habitat of the Cape of Good Hope it most likely is not *S. obliquidens*. It appears under the *S. obscurus* synonymy as an unjustified emendation of *Clymene similis* Gray, 1868 (= *Delphinus obscurus* Gray, 1828).

Delphinus chilensis Philippi, 1895:283. Appears in *Sagmatias australis* synonymy but was examined by R.L.B. who determined that the specimen cannot be identified as a synonym of *Lagenorhynchus australis*, but rather it should be defined as “Delphinid sp.”

Lagenorhynchus Fitzroyi: Lahille, 1899:200. Appears in *Sagmatias cruciger* synonymy but was misidentified by Lahille (1899) as *Lagenorhynchus Fitzroyi* Waterhouse, 1838 [= *Sagmatias obscurus* (Gray, 1828)]. It also appears in the synonymy of *S. obscurus*.

Misidentifications Found Within Synonymies of Other Genera (Not Lagenorhynchus)

Junior synonyms of *Cephalorhynchus commersonii* (Lacépède, 1804):

L[agenorhynchus]. Burmeisteri Moreno, 1892:390

Lagenorhynchus Floweri Moreno, 1892:385, Plates 8–9

Name combination for *Cephalorhynchus commersonii* (Lacépède, 1804):

Lag[enorhynchus]. burmeisteri Bierman and Slijper, 1947:1358

Misidentification of *Cephalorhynchus commersonii* (Lacépède, 1804):

Lagenorhynchus cruciger? Bruce, 1915:500, Plate 1

Name combination for *Peponocephala electra* (Gray, 1846):

Lagenorhynchus Electra Gray, 1846b:35, Plate 13

L[agenorhynchus] electra Flower, 1884:490, 511

Lagenorhynchus electra Flower, 1885:23

Electra electra Nakajima and Nishiwaki, 1965:65, Figures 1–8, Plates 1–7

Junior synonyms of *Peponocephala electra* (Gray, 1846):

Lagenorhynchus Asia Gray, 1846b:35, Plate 14

Electra Asia Gray, 1868b:7, Table 14

Electra fusiformis Gray, 1868b:7

Electra obtusa Gray, 1868b:7, Plate 13

Delphinus (Lagenorhynchus) fusiformis Owen, 1869:22, Plate 5 Figure 1

Phocaena pectoralis Peale, 1849:32, Plate 6 Figure 1

Delphinus pectoralis Cassin, 1858:28, Plate 5 Figure 2

Lagenorhynchus pectoralis Hershkovitz, 1966:70. Hershkovitz lists this name combination under the synonymy of “*Lagenorhynchus electra* Gray” and provides the authority of Cassin, 1858:28, however Cassin on page 28 lists *Delphinus pectoralis* (see above).

Junior synonym of *Lissodelphis borealis* (Peale, 1849) or *Lissodelphis peronii* (Lacépède, 1804):

Lagenorhynchus Thicolea Gray, 1846b:Plate 36. Photographs of the holotype of this specimen (a skull with the catalog no. 1849.5.25.5 at the British Museum (Natural History), London, online catalog accessed August 10, 2018) have been examined by R.L.B. and verified as *Lissodelphis* spp.

Name combination for *Lissodelphis borealis* (Peale, 1849) or *Lissodelphis peronii* (Lacépède, 1804):

Lagenorhynchus thicolea Flower, 1885:28

Electra thicolea Gray, 1868b:7, Plate 36

C[lymenia]. (Electra) thicolea Flower, 1884:512

Junior synonym of *Stenella coeruleoalba* (Meyen, 1833):

Lagenorhynchus caeruleo-albus Gray, 1850a:100

Lagenorhynchus lateralis Cassin, 1858:32, Plate 7 Figure 1

Incorrect subsequent spelling of *Lagenorhynchus caeruleo-albus* Gray, 1850 [= *Stenella coeruleoalba* (Meyen, 1833)]:

Lagenorrhynchus coeruleo-albus Burmeister, 1867:307

Received: 19 October 2017

Accepted: 15 November 2018

SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12573/supinfo>.

Table S1. List of specimens used for meristic data for this study. All specimens are from the Smithsonian Institution's National Museum of Natural History and catalog numbers are given.