

GENETIC VARIATION OF *KOGIA* SPP. WITH PRELIMINARY EVIDENCE FOR TWO SPECIES OF *KOGIA SIMA*

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ABSTRACT

Concordance between mitochondrial DNA (mtDNA) markers and morphologically based species identifications was examined for the two currently recognized *Kogia* species. We sequenced 406 base pairs of the control region and 398 base pairs of the cytochrome *b* gene from 108 *Kogia breviceps* and 47 *K. sima* samples. As expected, the two sister species were reciprocally monophyletic to each other in phylogenetic reconstructions, but within *K. sima*, we unexpectedly observed another reciprocally monophyletic relationship. The two *K. sima* clades resolved were phylogeographically concordant with all of the haplotypes in one clade observed solely among specimens sampled from the Atlantic Ocean and with those in the other clade observed solely among specimens sampled from the Indo-Pacific Ocean. These apparently allopatric clades were observed in all phylogenetic reconstructions using the maximum parsimony, maximum likelihood, and neighbor-joining algorithms, with the mtDNA gene sequences analyzed separately and combined. The nucleotide diversity for the combined gene sequence haplotypes of the two *K. sima* clades resolved in our analyses was 0.58% and 1.03% for the Atlantic and Indo-Pacific, respectively, whereas for the two recognized sister species, nucleotide diversity was 1.65% and 4.02% for *K. breviceps* and *K. sima*, respectively. The combined gene sequence haplotypes have accumulated 44 fixed base pair differences between the two *K. sima* clades compared to 20 fixed base pair differences between the two recognized sister species. Although our results

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are consistent with species-level differences between the two *K. sima* clades, recognition of a third *Kogia* species awaits supporting evidence that these two apparently allopatric clades represent reproductively isolated groups of animals.

Key words: dwarf sperm whale, pygmy sperm whale, *Kogia breviceps*, *Kogia sima*, mtDNA, control region, cytochrome *b*, phylogeny, cetaceans.

No study has yet characterized the geographic variability in morphological or molecular genetic markers for the two extant *Kogia* species, but morphological differences distinguish the pygmy sperm whale, *Kogia breviceps*, from the dwarf sperm whale, *K. sima* (Handley 1966; nomenclature after Rice 1998). Comparatively, *K. breviceps* is larger in both total body length and weight, has a smaller dorsal fin located farther back on the body, has no maxillary teeth, and has more mandibular teeth than *K. sima*. While distinctive, the external morphological characters can be confusing and lead to incorrect species identifications, especially among younger animals. However, several skull and postcranial skeleton characters can be used to accurately identify a specimen of any age (*e.g.*, maximum condylobasal length, rostrum length relative to its breadth, length, and shape of the mandibular symphysis, dentition patterns, and tooth morphology). Additional analyses of morphological data have supported Handley's (1966) conclusion of two extant species in the family Kogiidae, and the existence of these two species is widely accepted (Ross 1979, Nagorsen 1985, Caldwell and Caldwell 1989, Rice 1998, McAlpine 2002).

In addition to being morphologically distinctive, biological data indicate that the two *Kogia* species occupy different ecological niches. Patterns of distribution inferred from stranding records and at-sea sightings show that both species occupy all ocean basins with *K. sima* inhabiting predominantly tropical waters and *K. breviceps* inhabiting both tropical and temperate waters (Ross 1979; Caldwell and Caldwell 1989; Hill and Barlow 1992; Breese and Tershey 1993; Mullin *et al.* 1994; Ballance and Pitman 1998; Kinzey *et al.* 1999, 2000; Lucas and Hooker 2000; NOAA²). Epi-, meso- and bathy-pelagic prey have been identified among the stomach contents recovered from both *Kogia* species, but differences in composition of prey species suggest partitioning of their preferred habitats at sea (Raun *et al.* 1970; Ross 1979, 1984). Little else is known about the ecology of these species, and because there are so few at-sea sightings, patterns of patchiness in animal density or distribution cannot be inferred for either species. While the accumulation of morphological and biological data has continued to document and confirm differences between the *Kogia* species, population structure within ocean basins is unknown, and there are no data to suggest there may be discrete, isolated, perhaps uniquely adapted, populations of animals within the range of either species. Published mitochondrial DNA (mtDNA) control region and cytochrome *b* gene sequences also readily distinguish the two *Kogia* species. However, only three mtDNA control region and four cytochrome *b* gene sequences have been published in GenBank and are used for molecular genetic identification of species (Reeves *et al.* 2004), and concordance between these markers and the morphological characteristics of each species throughout their range has not been examined.

² Unpublished data, NOAA, National Marine Fisheries Service, Southwest Region Stranding Network, Long Beach, CA 90802, U.S.A. and Southeast Region Stranding Network, Miami, FL 33149, U.S.A.

Here, we present the first data documenting the inter- and intraspecific genetic variability of the mtDNA control region and cytochrome *b* gene for the family Kogiidae. We collected samples from *K. breviceps* and *K. sima* from many locations throughout their range and examined the concordance between genetic markers, morphology, and geography.

METHODS

We sequenced 108 samples of *K. breviceps* and 47 samples of *K. sima* collected between 1966 and 2001 from animals found stranded or incidentally taken in fisheries and identified to species using morphological characters (Fig. 1). The samples represent animals of both species inhabiting the Pacific Ocean (29 *K. breviceps*, 12 *K. sima*), Atlantic Ocean (72 *K. breviceps*, 31 *K. sima*), and Indian Ocean (7 *K. breviceps*, 4 *K. sima*). The Indian Ocean samples were all collected along the shores of South Africa, and similarly, our only southern hemisphere Atlantic Ocean samples were collected along South Africa's Atlantic seaboard (2 of 72 *K. breviceps* and 1 of 31 *K. sima*) (see inset, Fig. 1). The boundary between the Atlantic and Indian oceans is formed where the Agulhas and Benguella currents meet off South Africa and typically extends southwest from approximately Cape Town, South Africa.

Samples of skin, muscle, and internal organs ($n = 153$) were preserved in a 20% dimethylsulphoxide solution saturated with NaCl (Amos and Hoelzel 1991, Amos 1997), and teeth or bone ($n = 2$) were stored dry. All samples are archived at the Southwest Fisheries Science Center (SWFSC; contact author SJC for information).

DNA Extraction, PCR Amplification and Sequencing

Genomic DNA was extracted using CTAB (cetyltrimethylammonium bromide; Winnepenninckx *et al.* 1993), lithium chloride (Gemmell and Akiyama 1996), or phenol-chloroform (Sambrook *et al.* 1989) extraction protocols. The CTAB protocol successfully extracted DNA from a majority of our samples, and when CTAB was unsuccessful, one of the other protocols was used to extract DNA. Typically, the more degraded samples in our sample set yielded higher DNA concentrations with the phenol-chloroform based protocol. A fourth protocol, which was also phenol-chloroform based, was used to extract DNA from the tooth and bone samples (Hagelberg 1994). Following extraction, 406 base pairs of the 5' end of the hypervariable mtDNA control region and 398 base pairs of the 5' end of the mtDNA cytochrome *b* gene were amplified (Saiki *et al.* 1988) using primers³ H153 and L15812 for the control region and primers H15034 and L14570 for cytochrome *b* (see Table 1 for primer sequences). Because the bone samples yielded somewhat degraded DNA in fairly low concentrations (<10 ng), complete sequences were obtained by amplifying two overlapping, smaller fragments. For the control region, primers H16247 and L15812 were used to amplify one fragment and primers H153 and L16038 were used for the second fragment. Similarly, for cytochrome *b*, primers H14894 and L14570, and primers H15034 and L14698 were used to amplify the first and second fragments, respectively. Cycle sequencing was performed using Applied Biosystems Inc. dye terminator sequencing reagents and protocols. Primers H16343 and L15812 were used for the control region with

³ All primer names reference their position in the mtDNA sequence of the fin whale (Árnason *et al.* 1991).

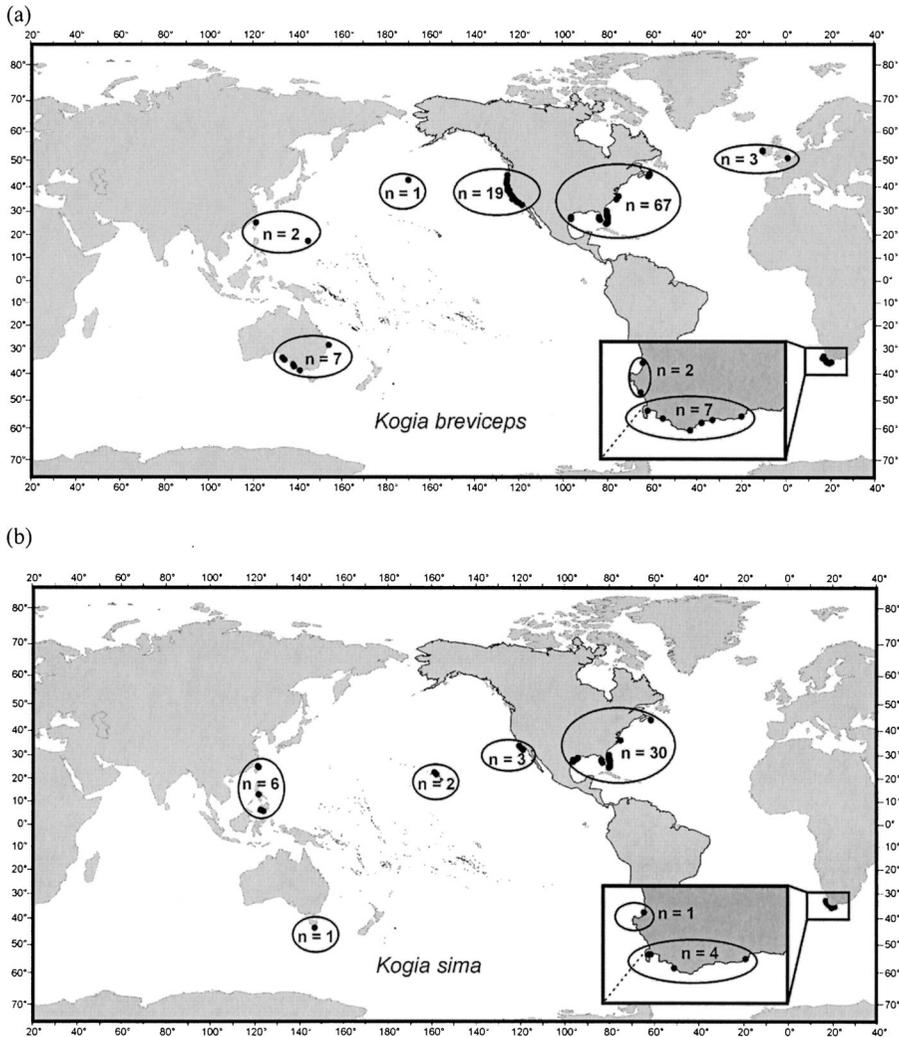


Figure 1. Geographic distribution of the *Kogia* species specimens used in our phylogenetic analyses. The sample locations were plotted for each specimen of (a) *Kogia breviceps* and (b) *K. sima* sequenced for the study. The inset in each map shows where samples were collected around South Africa. This region is important with respect to our analyses because the boundary separating the Indian Ocean and the Atlantic Ocean extends southwest from Cape Town, South Africa (dashed line indicates the approximate location of the boundary). The Indian Ocean samples were those collected near and to the east of Cape Town, and those collected to the west were from the Atlantic Ocean.

primer pairs H16343 and L16038, and H16247 and L15812 used for the reamplified product. Primers H15034 and L14570 were used for cytochrome *b* with primer pairs H15034 and L14698, and H14894 and L14570 used for the reamplified product. Both strands of the amplified DNA product of each specimen were sequenced independently as mutual controls using standard protocols on the Applied Biosystems Inc. model 377 sequencer. All sequences were the same length:

Table 1. Primer names and their sequences used to sequence the mitochondrial DNA control region and cytochrome *b* gene. The "H" and "L" designate heavy and light strand primers, respectively.

| Primer name | Gene region | Primer sequence | Source/Reference |
|-------------|-------------|--------------------------------|---------------------------------|
| H153 | Control | 5'-aaatacayacaggyccagcta-3' | Developed at SWFSC ^a |
| H14894 | Cyt b | 5'-ctccgtctacttcttatacc-3' | Developed at SWFSC |
| H15034 | Cyt b | 5'-cagaatgatattgtcctca-3' | Kocher <i>et al.</i> 1989 |
| H16247 | Control | 5'-ttgctggtttcacgcgg-3' | Developed at SWFSC |
| H16343 | Control | 5'-cctgaagtaagaaccagatg-3' | Rosel <i>et al.</i> 1994 |
| L14570 | Cyt b | 5'-tgacttgaaraaccaycgttg-3' | Martin and Palumbi 1993 |
| L14698 | Cyt b | 5'-catgatgAaacttcggctcc-3' | Developed at SWFSC |
| L15812 | Control | 5'-cctccctaagactcaagg-3' | Developed at SWFSC |
| L16038 | Control | 5'-catgctatgtataactgtgcattc-3' | Developed at SWFSC |

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406 base pairs for the control region and 398 base pairs for cytochrome *b*, and were aligned to published sequences using SEQED, version 1.0.3 software (Applied Biosystems, Inc. 1992).

Data Analysis

We reconstructed phylogenies for the *Kogia* species using only one representative of each haplotype identified in our data set, and the closest relative to *Kogia*, the sperm whale, *Physeter macrocephalus*, was used to root the trees. We generated phylogenies using the unweighted maximum parsimony, maximum likelihood and neighbor-joining algorithms in the program Phylogenetic Analysis Using Parsimony (PAUP), version 4.0 (Swofford 1993) and used 1,000 bootstrap replicates to estimate branch support. For the unweighted maximum parsimony analyses, exhaustive and branch-and-bound parsimony searches were not conducted, and no branch swapping was done during the bootstrap because of the number of closely related haplotypes for each species. For the maximum likelihood analyses, the 2-parameter Felsenstein (1984) substitution model was used with rates set equal for all sites using the empirical base frequencies and with transition-to-transversion ratios set at 2:1 and 10:1. The model was run with stepwise addition of sequences, and the Jukes and Cantor distance model was used to calculate the least squared fit. For the neighbor-joining phylogenetic reconstruction, genetic distances were the absolute number of base pair differences between haplotypes. Haplotypes were identified using MacClade, version 3.08a (Maddison and Maddison 1992), and genetic variation was quantified by (1) the average number of base pair differences between unique haplotypes, (2) nucleotide diversity, and (3) haplotypic diversity (Nei and Tajima 1981, Nei 1987) using Arlequin, version 2.0 (Schneider *et al.* 2000).

RESULTS

The mtDNA markers we sequenced are not independent and, therefore, we examined phylogenetic reconstructions using haplotypes identified among the

cytochrome *b* and control region sequences separately before combining them in the final analyses. The tree length and consistency indices for the phylogenies revealed that the tree length was much shorter using the cytochrome *b* sequences (*i.e.*, 237 *vs.* 607 in cytochrome *b* and control region, respectively), and that the consistency index was higher (*i.e.*, 0.527 *vs.* 0.282 in cytochrome *b* and control region, respectively). We considered this was evidence that the cytochrome *b* gene is more conservative for the deeper branches within the tree and, therefore, the more reliable marker for reconstructing the phylogenetic relationships of *Kogia*. However, phylogenetic reconstructions using either marker independently revealed three clades. All *K. breviceps* haplotypes were in one clade, and all *K. sima* haplotypes were in two clades, which had identical membership in all phylogenetic reconstructions and are referred to as *K. sima*-A and *K. sima*-B. In the unweighted parsimony analyses using cytochrome *b* sequences, the two extant species were sister to each other, and the *K. sima*-A and *K. sima*-B clades were also sister to each other. Each of these clades had strong bootstrap support (*i.e.*, 100%), and the node joining the two *K. sima* clades was strongly supported (89%). Although the unweighted parsimony analyses of the control region sequences resolved the same three clades, they had slightly different relationships to each other. That is, the *K. breviceps* and *K. sima*-A clades were sister to each other to the exclusion of the *K. sima*-B clade. However, in light of the relatively low (76%) bootstrap support for the node joining *K. breviceps* to *K. sima*-A, combined with the lower consistency index for the control region tree overall (*i.e.*, 0.282), we think that the monophyly of the nominal species is not seriously in doubt, and that the relationships reflected in the cytochrome *b* and, subsequently, the combined marker analyses, are reliable.

Phylogenetic reconstructions using parsimony, maximum likelihood, and neighbor-joining algorithms generated the same overall phylogeny for the combined cytochrome *b* and control region haplotypes as they did for each of the sequence data sets and, therefore, we present only the phylogram from the unweighted parsimony analysis with branch lengths and Bremer support indices for each clade resolved. Three clades, each with 100% bootstrap support, were resolved in all reconstructions (Fig. 2). As we observed in the cytochrome *b* sequence tree, the two *Kogia* species clades were reciprocally monophyletic, or sister, to each other, and there were reciprocally monophyletic clades within *K. sima*. No phylogeographically concordant clades were resolved within *K. breviceps*, indicating that from an evolutionary perspective sufficient gene flow has occurred between ocean basins to preclude the accumulation of genetic differences through drift and mutation. However, there were only two shared haplotypes between ocean basins suggesting contemporary female dispersal is likely limited (Appendix).

There were 74 *K. breviceps* (*i.e.*, 68% of the sequences) and 27 *K. sima* (*i.e.*, 57% of the sequences) haplotypes identified among the combined control region and cytochrome *b* gene sequences and used in the phylogenetic reconstructions (Appendix). When we compared the characteristics of these haplotypes among the three clades resolved, we found that the accumulated differences between *K. sima*-A and *K. sima*-B were greater than those accumulated between the two currently recognized *Kogia* species. That is, there were 44 fixed base pair differences, including six transversions, between the A and B clades of *K. sima* compared to 20 fixed base pair differences, including six transversions, between *K. breviceps* and *K. sima*. However, when we compared the sequence characteristics of *K. breviceps* to *K. sima*-A and to *K. sima*-B, there were 41 and 40 fixed base pair differences, including eight and nine transversions, respectively. Nucleotide diversity estimated from this data set was

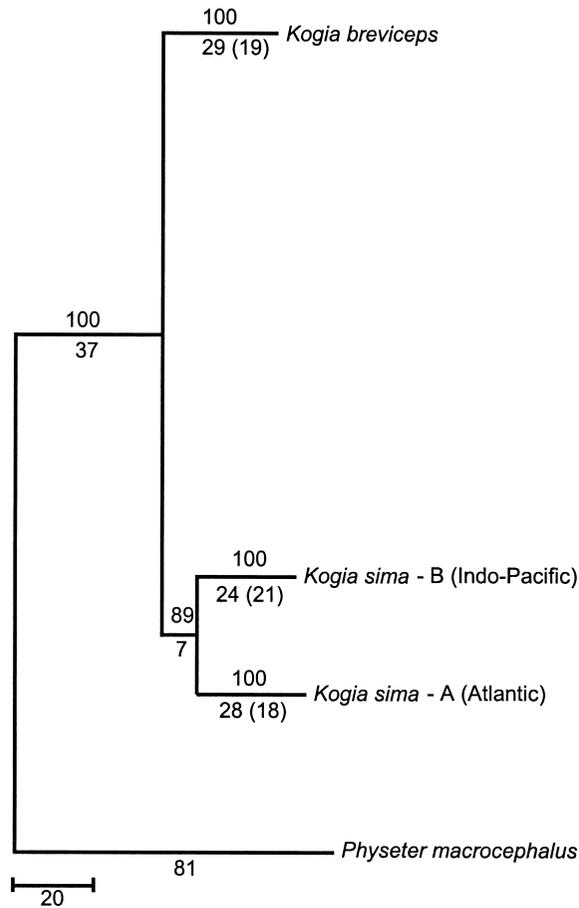


Figure 2. The unweighted maximum parsimony phylogram is shown here with branch lengths (below), Bremer support indices for each clade within *Kogia* (below and in parentheses) and the percentage of 1,000 bootstrap iterations supporting each node (above). The appropriate species name is written next to each clade resolved. The terminal branches were uninformative and removed from the illustration. The frequency of haplotypes in each clade is presented by ocean basin of sample origin in the Appendix.

highest for *K. sima* (i.e., 0.0402) than for each of the three clades resolved: 0.0165, 0.0058, and 0.0103 for *K. breviceps*, *K. sima*-A, and *K. sima*-B, respectively (Table 2, 3). The same pattern of genetic diversity was evident in each of the mtDNA gene regions sequenced, and we have included the sequence statistics for each region in Table 2. Overall, the estimated nucleotide diversity for *K. sima* is generally higher (~4%) than typically observed within odontocete species (~1%–2%; Baker *et al.* 1996, Leduc *et al.* 1999), while that for each *Kogia* clade is within the range typically observed.

DISCUSSION

The reciprocal monophyly we observed within *K. sima* identifies the clades as phylogenetic species (Fig. 2). These clades were resolved because the haplotypes

Table 2. Statistics for the mitochondrial DNA control region, cytochrome *b* and combined control region and cytochrome *b* sequence haplotypes identified in our data set. Standard deviations for each statistic are presented in parentheses.

| Species/ phylogenetic clades | Sample size (<i>n</i>) | Control region | | | Cytochrome <i>b</i> | | | Combined control region and cytochrome <i>b</i> | | |
|--|--------------------------------|----------------------------|-------------------------|------------------------------------|----------------------------|-------------------------|------------------------------------|--|-------------------------|------------------------------------|
| | | Haplotypes (<i>n</i>) | Nucleotide diversity | Average pairwise differences | Haplotypes (<i>n</i>) | Nucleotide diversity | Average pairwise differences | Haplotypes (<i>n</i>) | Nucleotide diversity | Average pairwise differences |
| <i>K. breviceps</i> | 108 | 65 | 0.0252 (0.0129) | 10.12 (4.66) | 37 | 0.0076 (0.0044) | 3.034 (1.594) | 74 | 0.0165 (0.0083) | 13.154 (5.966) |
| <i>K. sima</i> | 47 | 24 | 0.0436 (0.0219) | 17.476 (7.905) | 20 | 0.0367 (0.0186) | 14.614 (6.661) | 27 | 0.0402 (0.0198) | 32.091 (14.252) |
| <i>K. sima</i> – A (Atlantic Ocean) | 31 | 11 | 0.0069 (0.0042) | 2.748 (1.497) | 7 | 0.0047 (0.0031) | 1.867 (1.098) | 12 | 0.0058 (0.0032) | 4.615 (2.3274) |
| <i>K. sima</i> – B (Indo-Pacific Ocean) | 16 | 13 | 0.0135 (0.0077) | 5.433 (2.762) | 13 | 0.0070 (0.0044) | 2.792 (1.556) | 15 | 0.0103 (0.0056) | 8.225 (4.0257) |

Table 3. The average pairwise differences between the combined mitochondrial DNA control region and cytochrome *b* haplotypes for each clade resolved in phylogenetic reconstructions are in the cells below the diagonal and the within clade differences are on the diagonal. The number of fixed base pair differences between haplotypes in each clade, are in the cells above the diagonal, with the number of fixed transversions in parentheses.

| Species/phylogenetic clades | Species/phylogenetic clades | | |
|---|-----------------------------|---------------------------------|-------------------------------------|
| | <i>K. breviceps</i> | <i>K. sima</i> – Atlantic Ocean | <i>K. sima</i> – Indo-Pacific Ocean |
| <i>K. breviceps</i> | 13.154 | 40 (9) | 41 (8) |
| <i>K. sima</i> – A (Atlantic Ocean) | 75.073 | 4.615 | 44 (6) |
| <i>K. sima</i> – B (Indo-Pacific Ocean) | 80.615 | 63.623 | 8.225 |

share unique combinations of character states that could only have arisen within reproductively cohesive units (Cracraft 1987, 1997). Furthermore, the large number of fixed differences between the haplotypes in each clade suggests they have been differentiating for many generations such that lineage sorting is well advanced. However, there are three primary limitations to our study that keep us from concluding that the two *K. sima* clades represent two separate biological species. First, the two clades within *K. sima* are allopatric in our data set with all clade A haplotypes identified from specimens collected in the Atlantic Ocean, and with all clade B haplotypes identified from specimens collected in the Indian or Pacific Oceans. However, there are only five samples collected around the southern coast of South Africa (Fig. 1). This area is the most likely corridor for dispersal between ocean basins, and the collection locales for the nominal Atlantic Ocean and Indian Ocean samples from South Africa were collected only approximately 100 km apart. Second, in addition to having only a small number of specimens collected around South Africa, we had no samples from elsewhere in the South Atlantic and Indian Oceans, and thus have only a limited geographic representation of haplotypes for the *Kogia* species. Third, we used only one neutral, maternally inherited genetic marker, which is not sufficient to identify a biological species (Milinkovitch *et al.* 2001). If additional sampling confirms that the two groups of *K. sima* are indeed allopatric, the taxonomic implications are unclear. One possibility is that the genetic differences accumulated in isolation are maintained by oceanographic barriers, and that they may disappear if contact were reestablished. Alternatively, reproductive isolating mechanisms or a mode of competitive exclusion may have arisen, and these groups represent biological species. The evidence we present here needs to be accompanied by species-level differences in multiple independent markers (*i.e.*, either genetically unlinked molecular markers or morphological characters or both) before a third species of *Kogia* can be recognized (Reeves *et al.* 2004).

Although our limited knowledge about *Kogia* makes it difficult to explain fully the reciprocal monophyly we observed within *K. sima*, any explanation must take into account the biogeographic history and ecology of the species. During the Pleistocene, the Cape of Good Hope was an intermittent barrier to movement of tropical species between the Atlantic and Indo-Pacific Oceans (Davies 1963) and, as one example, Perrin *et al.* (1978, 1981) hypothesized that speciation within tropical *Stenella* species resulted from isolation of populations occupying Atlantic

and Indo-Pacific Ocean warm-water habitats during glacial maxima events in the Pleistocene. In this scenario, cool ocean temperatures during glacial maxima would have limited movement of *K. sima*, which is a predominantly tropical species, around the Cape, causing the Atlantic and Indo-Pacific populations to be isolated and to diverge genetically. The cool waters would not have limited movement of the more temperate *K. breviceps*, thus allowing evolutionarily significant gene flow to continue between the Atlantic and Indo-Pacific Oceans.

Contemporary oceanographic features associated with the Cape of Good Hope may limit animal movement between the Atlantic and Indo-Pacific Oceans. The warm-water Agulhas Current and cool-water Benguella Current define the boundary that effectively separates the Indian and Atlantic Oceans, and Ross (1984) proposed that this current boundary limits the distribution of *K. sima* around South Africa's coastline. Central to our discussion is the apparent allopatry of the two *K. sima* clades in our analyses, which needs, at least, to be better documented by additional samples from around South Africa. If additional sampling reveals a zone of sympatry for the two groups of haplotypes, reproductive isolation can be more directly tested by using independent molecular or morphological markers. Fixed differences between sympatric forms in multiple markers would be strong evidence for reproductive isolation. However, if allopatry of the clades is borne out by additional samples, additional markers need to be analyzed to determine whether the observed genetic divergence was paralleled by the evolution of reproductive isolating mechanisms. In other words, is the allopatry of the clades due to simple drift within isolated populations, or is there competitive exclusion preventing biological species from becoming established in the other's ocean basin?

The extreme divergence (8%) we observed between *K. sima* clades indicates long-term isolation of the groups. Conservatively assuming the molecular clock generally accepted for mammals (2% divergence/my; Wilson *et al.* 1985), the *K. sima* clades diverged approximately 4 mya, during the early Pliocene. One could argue that this represents ample time for climatic fluctuations to have repeatedly altered current patterns around the Cape of Good Hope such that dispersal was intermittently possible for species adapted to tropical ecosystems. If this is true, then one could infer that the geographic discreteness of the clades is largely the result of reproductive isolation and competitive exclusion. The reconstructed phylogeny and the proximity of samples belonging to *K. sima*'s A and B clades around South Africa may be interpreted as representing a pattern consistent with a mode of reproductive isolation being present. That is, because the apparent separation of the distributions is only approximately 100 km around the tip of South Africa, animals belonging to clades A and B may be considered essentially parapatric, or possibly sympatric, which necessarily means that the groups are reproductively isolated. Although the present-day oceanographic conditions appear unlikely to present a barrier to movement for *Kogia*, we lack data about the at-sea distribution of animals around the coast.

Although the two *K. sima* clades we identified fit the phylogenetic definition of a species, we stop short of concluding that a third *Kogia* species be recognized, because revision of the family Kogiidae's taxonomy requires supporting biological or molecular evidence of reproductive isolation to determine whether the "phylogenetic species" are on separate evolutionary trajectories. Pursuing additional research to resolve this apparent taxonomic uncertainty is important, because species are the fundamental unit of conservation.

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Appendix

The frequency of each haplotype is presented by ocean basin: Atlantic or Indo-Pacific for the two currently recognized species of *Kogia*. Each haplotype identified in our data set is numbered sequentially with GenBank and Southwest Fisheries Science Center (SWFSC) Genetics Archive accession numbers in accompanying columns. Two GenBank numbers are required for each haplotype; one each for the mitochondrial DNA control region and cytochrome *b* gene sequence. The “+” sign indicates a haplotype that occurs more than once in our data set, and only one sample identification number is listed.

| Haplotype number | GenBank accession # | SWFSC accession # | Atlantic Ocean | Indo-Pacific Ocean |
|--|---------------------|-------------------|----------------|--------------------|
| <i>Kogia breviceps</i> , pygmy sperm whale | | | | |
| 1 | AY943670/AY943759 | 0021+ | 1 | 1 |
| 2 | AY943671/AY943760 | 0024+ | 8 | 1 |
| 3 | AY943672/AY943761 | 0026+ | 4 | 0 |
| 4 | AY943673/AY943762 | 0029+ | 3 | 0 |
| 5 | AY943674/AY943760 | 0037+ | 2 | 0 |
| 6 | AY943676/AY943764 | 0767+ | 2 | 0 |
| 7 | AY943676/AY943760 | 2508+ | 2 | 0 |
| 8 | AY943681/AY943760 | 4462+ | 8 | 0 |
| 9 | AY943683/AY943761 | 4912+ | 2 | 0 |
| 10 | AY943684/AY943762 | 4913+ | 2 | 0 |
| 11 | AY943691/AY943760 | 7427+ | 4 | 0 |
| 12 | AY943718/AY943782 | 14186+ | 4 | 0 |
| 13 | AY943734/AY943761 | 23624+ | 2 | 0 |
| 14 | AY943675/AY943763 | 68 | 0 | 1 |
| 15 | AY943677/AY943762 | 1298 | 0 | 1 |
| 16 | AY943678/AY943767 | 1414 | 0 | 1 |
| 17 | AY943679/AY943760 | 1544 | 0 | 1 |
| 18 | AY943671/AY943768 | 3943 | 1 | 0 |
| 19 | AY943680/AY943769 | 3983 | 1 | 0 |
| 20 | AY943732/AY943770 | 3984 | 1 | 0 |
| 21 | AY943682/AY943765 | 4554 | 0 | 1 |
| 22 | AY943683/AY943771 | 5055 | 1 | 0 |
| 23 | AY943685/AY943772 | 5057 | 1 | 0 |
| 24 | AY943686/AY943762 | 6617 | 0 | 1 |
| 25 | AY943687/AY943762 | 7021 | 1 | 0 |
| 26 | AY943670/AY943773 | 7399 | 0 | 1 |
| 27 | AY943688/AY943774 | 7421 | 1 | 0 |
| 28 | AY943689/AY943763 | 7423 | 1 | 0 |
| 29 | AY943690/AY943766 | 7424 | 1 | 0 |
| 30 | AY943672/AY943775 | 7426 | 1 | 0 |
| 31 | AY943692/AY943761 | 7428 | 1 | 0 |
| 32 | AY943693/AY943776 | 7430 | 1 | 0 |
| 33 | AY943694/AY943777 | 8517 | 0 | 1 |
| 34 | AY943684/AY943778 | 8676 | 1 | 0 |
| 35 | AY943695/AY943759 | 9532 | 0 | 1 |
| 36 | AY943696/AY943763 | 9567 | 0 | 1 |
| 37 | AY943697/AY943779 | 10110 | 1 | 0 |
| 38 | AY943698/AY943766 | 10111 | 1 | 0 |
| 39 | AY943699/AY943782 | 10117 | 1 | 0 |
| 40 | AY943700/AY943762 | 10119 | 1 | 0 |

Appendix. Continued.

| Haplotype number | GenBank accession # | SWFSC accession # | Atlantic Ocean | Indo-Pacific Ocean |
|---------------------------------------|---------------------|-------------------|----------------|--------------------|
| 41 | AY943701/AY943760 | 10256 | 1 | 0 |
| 42 | AY943702/AY943780 | 10257 | 1 | 0 |
| 43 | AY943703/AY943765 | 10401 | 0 | 1 |
| 44 | AY943704/AY943760 | 10406 | 0 | 1 |
| 45 | AY943705/AY943781 | 10407 | 0 | 1 |
| 46 | AY943670/AY943783 | 11180 | 1 | 0 |
| 47 | AY943706/AY943760 | 11182 | 1 | 0 |
| 48 | AY943707/AY943760 | 11183 | 1 | 0 |
| 49 | AY943708/AY943783 | 12479 | 0 | 1 |
| 50 | AY943709/AY943760 | 12697 | 1 | 0 |
| 51 | AY943710/AY943784 | 12771 | 0 | 1 |
| 52 | AY943711/AY943783 | 12970 | 0 | 1 |
| 53 | AY943712/AY943785 | 12971 | 0 | 1 |
| 54 | AY943732/AY943761 | 12972 | 0 | 1 |
| 55 | AY943713/AY943786 | 12973 | 0 | 1 |
| 56 | AY943714/AY943762 | 12974 | 0 | 1 |
| 57 | AY943715/AY943783 | 12975 | 0 | 1 |
| 58 | AY943716/AY943787 | 12976 | 0 | 1 |
| 59 | AY943717/AY943763 | 13464 | 0 | 1 |
| 60 | AY943719/AY943763 | 15537 | 0 | 1 |
| 61 | AY943720/AY943783 | 15539 | 0 | 1 |
| 62 | AY943721/AY943788 | 15542 | 0 | 1 |
| 63 | AY943722/AY943789 | 15543 | 1 | 0 |
| 64 | AY943723/AY943783 | 15544 | 0 | 1 |
| 65 | AY943724/AY943790 | 15547 | 0 | 1 |
| 66 | AY943681/AY943791 | 15548 | 0 | 1 |
| 67 | AY943725/AY943792 | 15551 | 1 | 0 |
| 68 | AY943726/AY943759 | 17127 | 0 | 1 |
| 69 | AY943727/AY943793 | 17361 | 1 | 0 |
| 70 | AY943728/AY943794 | 17818 | 1 | 0 |
| 71 | AY943729/AY943760 | 17819 | 1 | 0 |
| 72 | AY943730/AY943760 | 17852 | 0 | 1 |
| 73 | AY943731/AY943795 | 17853 | 0 | 1 |
| 74 | AY943733/AY943759 | 23257 | 0 | 1 |
| <i>Kogia sima</i> , dwarf sperm whale | | | | |
| 1 | AY943735/AY943796 | 0038+ | 17 | 0 |
| 2 | AY943737/AY943798 | 2662+ | 0 | 2 |
| 3 | AY943740/AY943802 | 7431+ | 3 | 0 |
| 4 | AY943743/AY943805 | 10122+ | 2 | 0 |
| 5 | AY943736/AY943797 | 69 | 0 | 1 |
| 6 | AY943738/AY943799 | 2663 | 0 | 1 |
| 7 | AY943739/AY943800 | 2670 | 0 | 1 |
| 8 | AY943735/AY943801 | 5056 | 1 | 0 |
| 9 | AY943741/AY943803 | 9562 | 0 | 1 |
| 10 | AY943742/AY943804 | 9563 | 0 | 1 |
| 11 | AY943744/AY943802 | 10260 | 1 | 0 |
| 12 | AY943745/AY943806 | 11044 | 0 | 1 |
| 13 | AY943746/AY943802 | 11175 | 1 | 0 |
| 14 | AY943747/AY943807 | 11177 | 1 | 0 |

Appendix. Continued.

| Haplotype number | GenBank accession # | SWFSC accession # | Atlantic Ocean | Indo-Pacific Ocean |
|------------------|---------------------|-------------------|----------------|--------------------|
| 15 | AY943748/AY943802 | 12696 | 1 | 0 |
| 16 | AY943749/AY943802 | 13338 | 1 | 0 |
| 17 | AY943745/AY943808 | 15108 | 0 | 1 |
| 18 | AY943750/AY943797 | 15496 | 0 | 1 |
| 19 | AY943751/AY943809 | 15538 | 0 | 1 |
| 20 | AY943745/AY943798 | 15540 | 0 | 1 |
| 21 | AY943752/AY943810 | 15541 | 0 | 1 |
| 22 | AY943753/AY943811 | 15545 | 0 | 1 |
| 23 | AY943754/AY943812 | 15546 | 1 | 0 |
| 24 | AY943755/AY943813 | 17104 | 1 | 0 |
| 25 | AY943756/AY943814 | 18656 | 0 | 1 |
| 26 | AY943757/AY943796 | 23300 | 1 | 0 |
| 27 | AY943758/AY943815 | 23604 | 0 | 1 |