Cytochrome *b* Nucleotide Sequences and the Identification of Five Primary Lineages of Extant Cetaceans

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Relationships among and within baleen and toothed whales were examined using the complete sequence of the mitochondrial cytochrome *b* gene. Based on parsimony analyses of conservative nucleotide substitutions, five primary evolutionary lineages of extant cetaceans were identified, one represented by baleen whales (Mysticeti) and four represented by odontocetes (toothed whales). Based on the most comprehensive representation of taxa, both cetaceans and artiodactyls, the most parsimonious relationship among the five lineages is (Mysticeti, Odontoceti (Platanistoidea (Physeteroidea (Ziphioidea (Delphinida))))). This relationship, however, is labile and sensitive to ingroup representation and the choice of outgroup. The short nodes among the five cetacean lineages suggest that the divergence among these lineages occurred over a narrow time period, a finding consistent with the limited fossil evidence that indicates a major cetacean radiation 30–34 Mya. The level of divergence among the five cetacean lineages, and that seen between cetaceans and artiodactyls, suggests that cetaceans and artiodactyls had a common ancestor ≈60 Mya.

Introduction

The order Cetacea (whales, dolphins, porpoises) includes three suborders, the extinct Archaeoceti and the two extant suborders Odontoceti (toothed whales) and Mysticeti (baleen whales). It is now universally acknowledged that extant cetaceans are monophyletic, but this relationship was not established until the late 1960s and early 1970s after reassessment of paleontological findings (Valen 1968) and the accumulation of chromosomal data that revealed pronounced karyological similarities among mysticetes and odontocetes (Arnason 1969, 1972, 1974, 1982a; Kulu 1972). Molecular studies have since provided a large body of information on the two extant suborders (Arnason 1982b; de Jong 1982; Goodman et al. 1982; Arnason, Höglund, and Widegren 1984; Goodman 1989), and analyses of complete mitochondrial gene sequences have identified artiodactyls as the closest relatives of cetaceans (Arnason, Gullberg, and Widegren 1991; Irwin, Kocher, and Wilson 1991; Arnason and Johnsson 1992; Douzery 1993; Cao et al. 1994; Graur and Higgins 1994; Irwin and Arnason 1994; Janke et al. 1994; Krettek, Gullberg, and Arnason 1995).

Although the results from molecular studies are for the most part congruent with anatomical studies, a sister group relationship between Cetacea and Artiodactyla cannot be confirmed with monophyly, but these data do associate cetaceans with ungulates in general (e.g., Ochrymowych and Lambertsen 1984; Prothero 1993). The relationships between extant cetaceans and the Archae-

oceti, by comparison, have not been established in detail. Recent reports on fossils of ancient swimming mammals (Gingerich et al. 1994; Thewissen, Hussain, and Arif 1994) have not helped to resolve this relationship, and the age of these archaeocete fossils (>50 Myr) has appeared old relative to the age of the presumed closest relatives of the Cetacea (Berta 1994; Novacek 1994).

The molecular relationships of extant mysticetes have been studied recently in considerable detail (Arnason, Gretarsdottir, and Widegren 1992; Adegoke, Arnason, and Widegren 1993; Arnason, Gullberg, and Widegren 1993; Arnason and Gullberg 1994). Two of these studies, one examining the complete mitochondrial DNA (mtDNA) control region (Arnason, Gullberg, and Widegren 1993) and the other the cytochrome *b* gene (Arnason and Gullberg 1994), included all extant mysticete species. These studies clarified several phylogenetic relationships among the mysticetes, most notably the existence of at least two species of minke whales and the close relationship between the families Eschrichtiidae (gray whales) and Balaenopteridae (rorquals).

In this paper we present new and complete mitochondrial cytochrome *b* sequences for 20 odontocete cetaceans. We have combined these data with existing information on mysticetes and artiodactyls in an effort to assess cetacean relationships at several levels of divergence as well as the relationship between cetaceans and artiodactyls. All currently recognized extant cetacean families are represented in our samples (with the possible exception of the genus *Lipotes,* should it eventually merit family status). The analysis makes it possible to further test the hypothesis of odontocete paraphyly, originally proposed by Milinkovitch, Ortí, and Meyer (1993), and the findings (Adachi and Hasegawa 1995)

that the cytochrome *b* relationships among baleen whales, sperm whales, and dolphins are sensitive both to sampling and to choice of outgroup. We selected the mitochondrial cytochrome *b* gene for this study because it is probably the best-sampled mitochondrial gene for mammals (Irwin, Kocher, and Wilson 1991; Ma et al. 1993; Arnason and Gullberg 1994; Irwin and Arnason 1994; Stanley, Kadwell, and Wheeler 1994; Arnason et al. 1995; Ledje and Arnason 1996). In addition, findings based on this gene have generally been in a good agreement with accepted phylogenies, even for ages of >60 Myr (Irwin and Arnason 1994).

Materials and Methods

The mysticete and sperm whale sequences included in the present study were reported previously (Arnason and Gullberg 1994). Other cetacean sequences were PCR amplified using the following primers (underlined regions represent restriction sites): L5′ AGGCGTCGAAGCTTG-ACATGAAAAGCCATCGTTG, L5′ ACAGTCGTG-AAGCTTCAACTACAAGAACAYTAATGA (light strand, *Hin*dIII); H5′ CGGAATTCCATTTTTGGTTTA-CAAGAC, H5′ AAGGAATTCTTTGGGTGCTGATGG-TGGAGT (heavy strand, *Eco*RI). After amplification, the product was cleaved with the appropriate restriction enzymes, electrophoresed on a preparative agarose gel, excised, electroeluted, and ligated into phage M13mp18/19. Sequencing of positive clones (plaque-hybridization) was according to the dideoxy protocol with ^{35}S-dATP. Sequencing was performed by the aid of several internal sequencing primers. The length of the gene is 1,140 bp in all species. Each final sequence constitutes a consensus of a minimum of three clones.

Nucleotide sequences were analyzed with PAUP version 3.1.1 (Swofford 1993). Distant relationships were analyzed on the basis of conservative nucleotide substitutions (CNS) (Irwin, Kocher, and Wilson 1991): i.e., all substitutions in codon position 1 (excluding leucine transitions), all substitutions in codon position 2, and transversional substitutions in codon position 3. CNS have been shown to provide results that are consistent with accepted phylogenetic relationships spanning a wide temporal range (Irwin, Kocher, and Wilson 1991; Graur and Higgins 1994; Irwin and Arnason 1994). They may, however, be somewhat insensitive for resolving closely related taxa. Therefore, the study of the Ziphiidae (beaked whales) and the Delphinoidea (Delphinidae, Monodontidae, Phocoenidae) plus the Amazon and La Plata river dolphins was complemented with analysis of unmodified sequences, i.e., equal weightings of all positions. The species included in our present study are listed in the legend of figure 1 where their EMBL accession numbers are also given. Users of

the cetacean sequences are obligatorily requested to refer to the present paper and not only to the accession numbers of the sequences.

Results

Parsimony Analysis of Conservative Nucleotide Substitutions

Figure 1 represents the results of a maximum parsimony analysis of CNS (Irwin, Kocher, and Wilson 1991) including 28 cetaceans, 10 artiodactyls, 1 perissodactyl (donkey), and the hedgehog (order Lipotyphla). Mysticete relationships have been detailed earlier (Arnason and Gullberg 1994), and three species of the family Balaenopteridae (fin whale, blue whale, humpback whale) were, therefore, not included in the analysis. Likewise one dolphin species, spotted dolphin, was not included. This species is closely related to the spinner and bottlenose dolphins. The artiodactyls were chosen randomly among species representing different evolutionary lineages. The resultant phylogenetic analysis depicted a relationship between cetaceans and the hippopotamus, but the bootstrap support for this relationship was limited (53) relative to other artiodactyls. The monophyly of cetaceans was supported by a bootstrap value of 100, and within this clade five discrete lineages were identified. The most parsimonious relationship among the taxa included in figure 1 was determined by a heuristic search applying random stepwise addition, 10 replicates. The strict consensus (50% majority rule) of 29 equally most parsimonious trees (length: 1,452, CI: 0.354, RI: 0.603) produced the following most parsimonious arrangement of the artiodactyl/cetacean relationship: (Camelidae ((Suidae, Tayassuidae) (Ruminantia) (*Hippopotamus* (Cetacca)))). The most parsimonious relationship among the five cetacean lineages was: (Mysticeti, Odontoceti (Platanistoidea (Physeteroidea (Ziphioidea (Delphinida)))))).

A monophyletic Mysticeti clade was supported with a bootstrap value of 99 (fig. 1). The present findings confirm the evolutionary position of the gray whale (family Eschrichtiidae) within the genus *Balaenoptera* of the family Balaenopteridae (rorquals), making genus *Balaenoptera* and the family Balaenopteridae paraphyletic.

A sister group relationship between sperm and pygmy sperm whales was supported with a bootstrap value of 92. No relationships between the sperm whales and the mysticete family Balaenopteridae (rorquals) were observed. Among the beaked whales (family Ziphiidae), a separate position of the Baird's beaked whale was recognized relative to the five other species, but the relationships among the other genera were unresolved. No
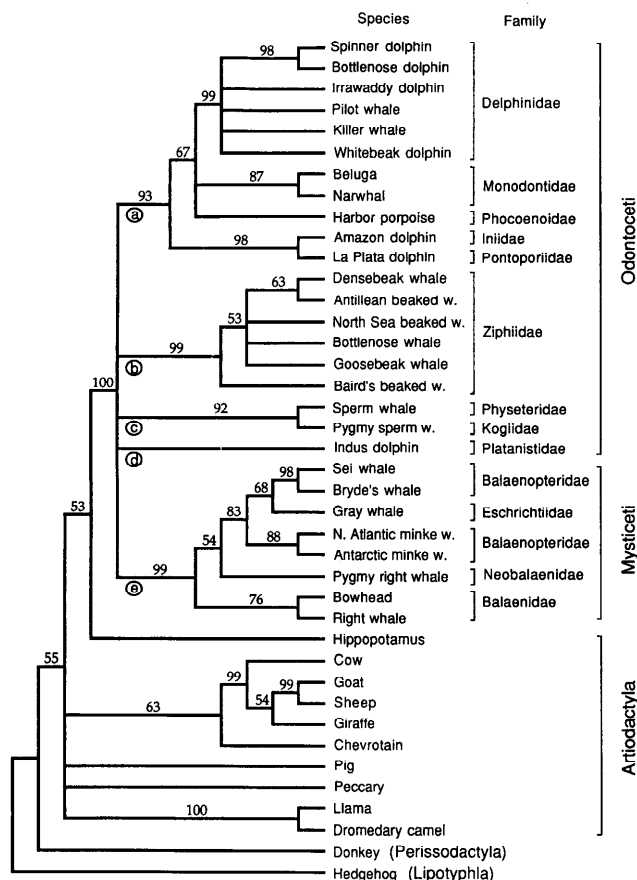
FIG. 1.—Majority-rule bootstrap consensus tree (heuristic search, maximum parsimony, 500 replicates) based on conservative nucleotide substitutions (Irwin, Kocher, and Wilson 1991) in the complete cytochrome *b* sequence (1,140 bp) of 28 cetaceans, 10 artiodactyls, and the donkey (order Perissodactyla), using the hedgehog (order Lipotyphla) as outgroup. Bootstrap values (50% majority rule) are included. The cetacean families are Delphinidae, dolphins; Monodontidae, narwhals; Phocoenidae, harbor porpoises; Iniidae, iniids; Pontoporiidae, pontoporiids; Ziphiidae, beaked whales; Physeteridae, sperm whales; Kogiidae, pygmy sperm whales; Platanistidae, platanistids; Balaenopteridae, rorquals; Eschrichtiidae, gray whales; Neobalaenidae, pygmy right whales; and Balaenidae, right whales. Other species are referred to by order. The analysis identifies five primary lineages of extant cetaceans, designated with encircled letters: a, Delphinida; b, Ziphioidea; c, Physeteroidea; d, Platanistoidea; and e, Mysticeti. The relationship among the five cetacean lineages is unresolved in bootstrap analyses, but with this representation of taxa, the most parsimonious relationship is outgroup (Mysticeti, Odontoceti (Platanistoidea (Ziphioidea (Physeteroidea (Delphinida))))). This relationship is sensitive, however, to both ingroup and outgroup representation. Delphinida includes the superfamilies Delphinoidea (with the families Delphinidae, Monodontidae and Phocoenidae) and Inioidea (with the families Iniidae and Pontoporiidae); Ziphioidea includes one extant family, Ziphiidae; Physeteroidea includes the families Physeteridae and Kogiidae; Platanistoidea includes one extant family, Platanistidae. Mysticeti includes the extant families Balaenidae, Neobalaenidae, Eschrichtiidae, and Balaenopteridae. The sequences of the sperm whale and the mysticetes have been presented previously (Arnason and Gullberg 1994). The sequences of the llama and the dromedary camel are from Stanley, Kadwell, and Wheeler (1994), other artiodactyl sequences are from Irwin, Kocher, and Wilson (1991) and Irwin and Arnason (1994). The

close affinities were recognized between the Physeteridae (sperm whales) and the Ziphiidae (beaked whales).

The clade Delphinoidea + *Inia* + *Pontoporia* was supported by a high bootstrap value, 93. This clade corresponds to the infraorder Delphinida proposed by de Muizon (1988, 1994). There is a difference in opinion, however, as to whether *Inia, Pontoporia,* and *Lipotes* should be separated at the family level (de Muizon 1994) or be included in a single family with three different genera (Heyning 1989). This question will be addressed later, but in figure 1 the Amazon and La Plata dolphins have been separated at the family level. The position of the baji, *Lipotes vexillifer,* remains unsettled at this time as samples from this species were not available. The present analysis, nonetheless, revealed no affinities between the Indus dolphin (*Platanista minor*) and the Amazon and La Plata dolphins. The phylogenetic relationships among the Phocoenidae, Monodontidae, and Delphinidae were not resolved on the basis of CNS.

Parsimony Analysis Based on Nucleotide Substitutions in Unmodified Sequences

The two clades, Delphinida (Delphinidae, Phocoenidae, Monodontidae, *Inia,* and *Pontoporia*) and Ziphiidae (beaked whales), were represented by 12 and 6 species, respectively. In addition to parsimony analysis of CNS, the phylogenetic relationships within each clade were studied using two mysticetes as an outgroup in a parsimony analysis based on unmodified sequences, i.e., all nucleotide substitutions (fig. 2). This analysis also

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donkey sequence is from a complete mtDNA molecule of this species (Xu and Arnason, unpublished). The hedgehog sequence is also from a complete mtDNA molecule (Krettek, Gullberg, and Arnason 1995). The new cetacean sequences have been deposited at EMBL with accession numbers X92524–X92543. Users of all sequences produced by our laboratory are obligatorily requested to refer to the original papers where these sequences are described and not only to the accession numbers of the sequences. Cetacean species names: spinner dolphin, *Stenella longirostris*; bottlenose dolphin, *Tursiops truncatus*; Irrawaddy dolphin, *Orcaella brevirostris*; pilot whale, *Globicephala melaena*; killer whale, *Orcinus orca*; whitebeak dolphin, *Lagenorhynchus albirostris*; beluga, *Delphinapterus leucas*; narwhal, *Monodon monoceros*; harbor porpoise, *Phocoena phocoena*; Amazon dolphin, *Inia geoffrensis*; La Plata dolphin, *Pontoporia blainvillei*; densebeak whale, *Mesoplodon densirostris*; Antillean beaked whale, *M. europaeus*; North Sea beaked whale, *M. bidens*; bottlenose whale, *Hyperoodon ampullatus*; goosebeak whale, *Ziphius cavirostris*; Baird's beaked whale, *Berardius bairdii*; sperm whale, *Physeter macrocephalus*; pygmy sperm whale, *Kogia breviceps*; Indus dolphin, *Platanista minor*; sei whale, *Balaenoptera borealis*; Bryde's whale, *B. edeni*; gray whale, *Eschrichtius robustus*; North Atlantic minke whale, *Balaenoptera acutorostrata*; Antarctic minke whale, *B. bonaerensis*; pygmy right whale, *Caperea marginata*; bowhead, *Balaena mysticetus*; right whale, *B. glacialis*.
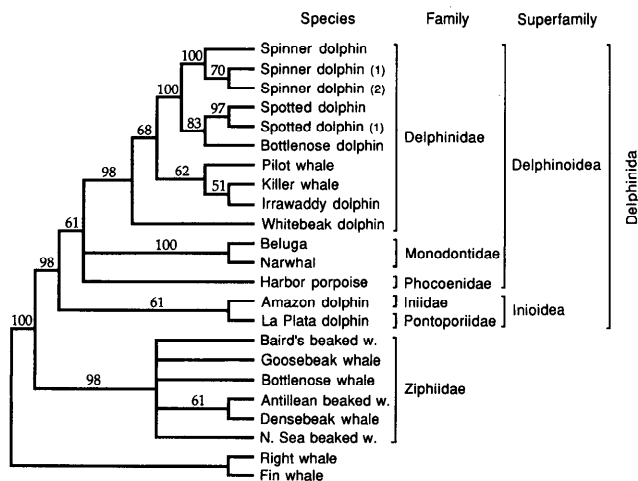
FIG. 2.—Majority-rule bootstrap consensus tree (heuristic search, maximum parsimony, 500 replicates) of 15 equally weighted (unmodified) cytochrome *b* sequences of the Delphinida and six beaked whales (family Ziphiidae), using two mysticetes as outgroup. Bootstrap values (50% majority rule) are included. Two sequences of spinner dolphin (1 and 2) and one of spotted dolphin (1) have been published previously (Irwin, Kocher, and Wilson 1991). The analysis does not conclusively resolve the relationship between the three families of Delphinoidea. The Irrawaddy dolphin is solidly nested among the delphinids, and there are no affinities between this species and the narwhal and the beluga (family Monodontidae). Generic distinctions among the beaked whales were not resolved. The spotted dolphin, *Stenella attenuata,* was not included among the species listed in the legend to figure 1.

included three sequences previously published by Irwin, Kocher, and Wilson (1991), two of the spinner dolphin (*Stenella longirostris*), and one of the spotted dolphin (*Stenella attenuata*). The most parsimonious relationship of the Delphinida sequences was ((*Inia, Pontoporia*) (Phocoenidae (Monodontidae (Delphinidae)))). A monophyletic family, Delphinidae, was supported by a bootstrap value of 98, but the relationship between the three delphinoid families (Phocoenidae, Monodontidae, Delphinidae) was not resolved. Among the Delphinidae, the whitebeak dolphin had a basal position relative to the other six species, which grouped into two clades, one comprising the Irrawaddy dolphin and the killer and pilot whales and the other containing the spinner, spotted, and bottlenose dolphins. The Irrawaddy dolphin was solidly nested among the Delphinidae, and no affinities were registered between this species and the Monodontidae (narwhals). The analysis notably did not separate the sequences of the spotted, spinner, and bottlenose dolphins according to their generic distinction. In a previous study (Irwin, Kocher, and Wilson 1991), based on CNS, one sequence of the spinner dolphin grouped with that of the spotted dolphin rather than with the conspecific sequence. The present analysis grouped all *Stenella*

sequences, including those of Irwin, Kocher, and Wilson (1991), according to species.

The parsimony analysis of CNS, like the analysis based on all nucleotide substitutions, provided only limited resolution for relationships among beaked whales. In the most parsimonious tree, the Baird's beaked whale and the goosebeak whale grouped together, but the bootstrap support for this arrangement was just below 50. None of the analyses supported the notion (Moore 1968) that the densebeak whale, *Mesoplodon densirostris,* is distantly related to other species of genus *Mesoplodon*.

Distances Among and Within Cetacean Clades

The present phylogenetic analyses addressed several evolutionary relationships that have been contended among cetologists. With the phylogenetic framework established on the basis of parsimony analysis, we examined the percent sequence difference among and within clades in order to investigate the congruence among these data, the present phylogenetic framework and common systematic classifications. Deeper divergences were examined on the basis of CNS, but within the clade Delphinida, which spans both distant and recent divergences, these data were complemented with the differences among complete sequences.

Table 1 shows the percent differences with respect to CNS among the complete cytochrome *b* sequences of one representative of each of the five primary cetacean lineages, eight artiodactyls, the donkey, and the hedgehog. The mean difference among the five cetacean lineages is 7.1%, and that between cetaceans and artiodactyls is 12.6% (11.9% between hippopotamus and the cetaceans).

Table 2 shows the percent differences among the cytochrome *b* sequences of the 12 Delphinida species with respect to both total nucleotide substitutions and CNS. Three families, Phocoenidae, Monodontidae, and Delphinidae, are acknowledged within the superfamily Delphinoidea. The nucleotide differences among the families Delphinidae and Monodontidae, and Delphinidae and Phocoenidae are 13.1% and 13.6%, respectively. The corresponding difference between Monodontidae and Phocoenidae is 14.8%. Between Delphinidae and Monodontidae the difference with respect to conservative nucleotide substitutions is 3.7%, and that between Delphinidae and Phocoenidae 4.4%, the same as that between Monodontidae and Phocoenidae. As evident in table 2, there is a distinct difference between the two river dolphins, the Amazon dolphin and the La Plata dolphin, and the three Delphinoidea families. The distinction between *Inia* and *Pontoporia* is also notable, as the difference between these two species is greater than that between the three acknowledged Delphinoidea fam

Table 1

Percent Differences (Conservative Nucleotide Substitutions) among Representatives of the Five Primary Cetacean Lineages, Eight Artiodactyls, Donkey, and Hedgehog

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 Fin whale	—	7.2	6.4	6.8	6.7	11.1	11.2	11.0	12.6	12.0	12.0	12.2	13.2	12.2	18.8
2 Sperm whale		—	7.4	7.9	7.8	12.7	12.8	13.8	14.0	13.2	13.7	13.2	13.3	13.3	19.1
3 Bottlenose whale ..			—	6.9	7.1	12.2	11.8	11.7	12.3	12.0	12.4	13.4	13.0	12.2	16.7
4 Indus dolphin				—	6.9	12.1	12.5	12.8	13.7	13.6	13.2	13.6	13.4	13.7	15.7
5 Bottlenose dolphin .					—	11.5	12.4	11.8	13.1	12.1	12.6	13.1	13.2	13.2	17.7
6 Hippopotamus						—	10.8	11.1	12.2	12.2	10.8	12.5	12.3	12.3	15.7
7 Cow							—	5.9	9.2	10.8	10.6	10.9	11.3	11.6	16.7
8 Goat								—	9.6	11.1	9.5	11.8	12.6	11.5	19.1
9 Chevrotain									—	10.8	11.0	11.1	12.2	12.1	17.4
10 Pig										—	8.9	11.1	11.1	11.4	16.9
11 Peccary											—	12.9	13.1	10.6	16.3
12 Llama												—	4.9	11.2	17.5
13 Dromedary camel .													—	11.2	18.2
14 Donkey														—	15.7
15 Hedgehog															

ilies, suggesting that the two species should be included in separate families.

CNS difference between the sperm and pygmy sperm whales is 5.6%. This value is considerably greater than that among the three families of the Delphinoidea (≈4%), suggesting that the sperm and pygmy sperm whales should be included in different families. CNS among the beaked whales are in the range 2.5%–3.8%, i.e., less than the difference among Delphinoidea families.

With the exception of a detailed comparison of the complete mtDNA molecules of the fin and blue whales (Arnason and Gullberg 1993), two species that on occasion have viable offspring (Arnason et al. 1991; Spilliaert et al. 1991), distance data on complete genes have not been previously presented for mysticetes. The total nucleotide and CNS differences between these two species are 7.7% and 1.5%, respectively. The gray whale

falls within the Balaenopteridae with respect to both total and CNS differences. Total nucleotide difference between the families Balaenidae and Balaenopteridae is ≈10%, whereas the corresponding CNS difference is 2%–2.5%. These differences, which are smaller than those among Delphinoidea families, imply a much more recent evolutionary divergence between the Balaenidae and other mysticetes than generally acknowledged.

Discussion

The phylogenetic analyses identified five clades of extant cetaceans. The phylogenetic relationships among the five clades were not resolved in the bootstrap analysis, but with the given cetacean and artiodactyl representation (fig. 1), the most parsimonious relationship of the five clades was (Mysticeti (Platanistidae (Physeteridae, Kogiidae (Ziphiidae (Delphinida))))). If this rela-

Table 2

Differences in Percent among the Complete (Unmodified) Cytochrome *b* Sequences of Delphinida Species. Above Diagonal: All Nucleotide Substitutions. Below Diagonal: Conservative Nucleotide Substitutions

Species	1	2	3	4	5	6	7	8	9	10	11	12
1 Spotted dolphin	—	4.2	4.3	7.3	7.8	8.2	8.6	13.3	12.3	13.4	16.0	17.4
2 Spinner dolphin ...	0.4	—	5.4	7.5	8.5	8.9	8.9	13.4	12.4	13.7	16.1	17.0
3 Bottlenose dolphin .	0.4	0.7	—	8.9	8.9	10.4	9.3	14.6	13.5	13.9	16.5	17.9
4 Pilot whale	1.8	1.8	2.1	—	6.6	7.8	8.5	13.6	11.6	13.7	16.3	16.2
5 Irrawaddy dolphin ..	1.7	1.6	1.8	1.4	—	7.1	8.9	13.4	12.5	13.4	15.7	16.8
6 Killer whale	1.8	1.8	1.9	2.3	1.6	—	9.1	13.1	13.1	13.7	17.2	17.1
7 Whitebeak dolphin .	1.7	1.6	1.7	1.8	1.4	1.9	—	12.5	12.0	13.5	15.3	16.4
8 Beluga	3.8	3.7	4.0	3.7	3.5	4.2	3.8	—	6.8	15.3	16.1	16.1
9 Narwhal	3.7	3.6	3.9	3.4	3.2	4.1	3.7	2.1	—	14.3	17.0	16.9
10 Harbor porpoise ...	4.3	4.4	4.5	4.4	4.2	4.5	4.3	4.6	4.2	—	15.7	17.7
11 Amazon dolphin ...	7.1	7.0	7.1	7.0	6.3	7.4	6.6	6.1	6.6	7.3	—	17.0
12 La Plata dolphin ...	7.8	7.7	8.0	7.7	7.4	8.1	7.4	7.3	8.1	8.2	7.7	—

tionship reflects true phylogeny, the primary evolutionary distinction among extant cetaceans is between the Mysticeti and the Odontoceti. It should be observed, however, that this distinction is not recognized in bootstrap analysis. The lack of resolution among the five cetacean clades is consistent with the similar distance values for CNS among the five clades. According to relative rate test, the rate of molecular evolution of the cytochrome *b* gene of the five lineages is similar.

The clade Delphinida was represented by 12 species in the present analysis (fig. 2). Within the superfamily Delphinoidea, the phylogenetic analysis identified the three acknowledged families, Phocoenidae (harbor porpoises), Monodontidae (narwhals), and Delphinidae (dolphins), but the interrelationship of the three families was not resolved conclusively in the bootstrap analysis. The most parsimonious relationship of the three families is (Phocoenidae (Monodontidae (Delphinidae))). It should be observed, however, that the family Phocoenidae was represented by only one species. An extended representation of members of this family might, therefore, improve the resolution of the analysis.

The phylogenetic analyses showed that within the clade Delphinida, the Amazon dolphin (*Inia geoffrensis*) and the La Plata dolphin (*Pontoporia blainvillei*) are distinct from the Delphinoidea. The two species are also distinct fom each other, as shown by the molecular difference betwcen the two species, which is markedly greater than that among the acknowledged Delphinoidea families. It should be observed, however, that according to relative rate test the rate of molecular evolution in cytochrome *b* has been faster in the Amazon and La Plata dolphins than in other Delphinida species. Nevertheless, the present analysis suggests that the Amazon dolphin and the La Plata dolphin should be separated at the level of family and joined in the superfamily Inioidea, a sister group to the Delphinoidea. The phylogenetic analysis supports the following relationship of the Delphinida families: ((Iniidae, Pontoporiidae) (Phocoenidae (Monodontidae (Delphinidae)))). The familial distinction between Iniidae and Pontoporiidae is consistent with the findings of de Muizon (1988).

Based on the present tree, the family Delphinidae is a distinct clade, consistent with the presence of a particular repeat length (1,580 bp) of a common cctaccan DNA-satellite that in all other cetaceans is characterized by a repeat length of ≈1,750 bp (Arnason, Höglund, and Widegren 1984; Widegren, Arnason, and Akusjärvi 1985; Gretarsdottir and Arnason 1993). The systematic position of the Irrawaddy dolphin within the Delphinoidea has been controversial. Its position within the family Delphinidae has been postulated previously on the basis of the presence of the 1,580-bp repeat of the common cetacean DNA-satellite and sequence analysis of

highly repetitive DNA (Gretarsdottir and Arnason 1992) and immunological (Lint et al. 1990) and electrophoretic studies (Shimura and Numachi 1987). The present data are consistent with those results. They are, however, inconsistent with the serological affinity recorded between Ziphiidae and Phocoenidae in the latter two studies.

The phylogenetic analysis based on CNS (fig. 1) did not record affinities between the Indus dolphin and the Amazon and La Plata dolphins. Our findings are congruent with both paleontological and anatomical data in supporting a distinction between the platanistids and inioids (de Muizon 1988, 1994; Heyning 1989; Fordyce 1994; Messenger 1994).

The resolution among the beaked whales (Ziphiidae) was limited in both our analyses of CNS and of unmodified sequences (figs. 1 and 2). The analyses suggested, albeit only weakly, that Baird's beaked whale is a sister taxon to the other genera included, an observation consistent with Heyning (1989). The difference among the ziphiid genera with respect to conservative substitutions is 2.5%–3.8%, i.e., less than that among Delphinoidea families. The parsimony analysis did not support Moore's (1968) suggestion of a distant position for the densebeak whale relative to othcr *Mesoplodon* species.

The parsimony analysis placed the sperm and pygmy sperm whales as sister taxa, but the sequences of the two species are strikingly distinct, which is consistent with data from both the mtDNA control region (Arnason, Gullberg, and Widegren 1993) and anatomical studies (Heyning 1989). Notably, the CNS difference between these two species, 5.6%, is considerably greater than that among the three families of the Delphinoidea (≈4%). These results support the proposal of Fordyce and Barnes (1994) that *Physeter* and *Kogia* should be included in different families. No affinity, however, was found between sperm and beaked whales, as proposed by de Muizon (1988, 1991), who included the sperm and beaked whales in the infraorder Physeterida.

Overall, the cytochrome *b* relationships of extant cetaceans suggest that the five primary clades have a comparable taxonomic rank. Although not singled out in the bootstrap analysis, we suggest that the subordinal rank of Mysticeti and Odontoceti is maintained, consistent with the most parsimonious cytochrome *b* relationship based on comprehensive cetacean and artiodactyl representation. Accordingly, the suborder Odontoceti includes four extant lineages: (1) Physeteroidea with the families Physeteridae and Kogiidae; (2) Ziphioidea with the family Ziphiidae; (3) Platanistoidea with the family Platanistidae; and (4) Delphinida with the superfamily Inioidea with the families Iniidae and Pontoporiidae (and possibly also the Lipotidae), and the superfamily Delphinoidea with the families Phocoenidae, Monodon-

tidae, and Delphinidae. We are aware that in this proposal we accept a difference in systematic distinction between that of infraorder (Delphinida) and superfamily (Physeteroidea, Ziphioidea, Platanistoidea). However, despite the fact that the four lineages are at a similar evolutionary level, we feel that the present data should be complemented by additional classical and molecular information before a new and more coherent systematic arrangement and nomenclature are proposed for extant odontocetes.

The existence of four odontocete clades is congruent for the most part with previous findings based on comparisons of facial and nasal anatomy (Heyning 1989; Heyning and Mead 1990). These authors identified the Platanistidae as a sister group to the Delphinida (as defined by de Muizon [1988]). The position of *Platanista* relative to other odontocete clades was not determined conclusively in the present analysis, but the most parsimonious relationship, based on a comprehensive representation of taxa, placed it as a sister taxon to the remaining odontocete clades. This position is sensitive, however, to changes in the representation of other taxa.

Mysticete mtDNA relationships have been addressed recently in two studies that included all extant species (Arnason, Gullberg, and Widegren 1993; Arnason and Gullberg 1994). These relationships have also been studied extensively on the basis of highly repetitive sequences of nuclear DNA (Arnason, Gretarsdottir, and Widegren 1992; Adegoke, Arnason, and Widegren 1993). The present phylogenetic analysis confirms the previously recognized position of the gray whale, *Eschrichtius robustus,* within the family Balaenopteridae (rorquals), a finding supported by comparisons of both total substitutions and CNS among mysticete cytochrome *b* sequences. Another noteworthy finding is the limited difference (both total and CNS) between the family Balaenidae (right whales) and remaining mysticetes, which suggests a much closer evolutionary relationship between these lineages than commonly acknowledged.

The recently accumulated cytochrome *b* data of cetaceans together with those of artiodactyls make it possible to examine various phylogenetic relationships that previously have been unaccessible. As mentioned earlier, the differences among the five primary cetacean lineages are very similar (table 1), and the bootstrap analysis based on CNS (fig. 1) does not conclusively resolve the evolutionary relationships among individual lineages. The findings are in agreement with analyses of the common cetacean DNA-satellite (Arnason, Höglund, and Widegren 1984; Gretarsdottir and Arnason 1993). Although the fossil record is not complete for all cetacean lineages, most paleontological evidence suggests

that the five extant primary lineages separated 30–34 Mya, being no older than the Eocene/Oligocene boundary at ≈34 Mya (E. Fordyce, personal communication). The paleontological records of putative mysticetes are traceable to more than 30 Mya, whereas the oldest described odontocetes are not clearly older than 30 Myr (Fordyce and Barnes 1994). By 30 Mya, however, odontocetes had diversified significantly. Therefore, the absence of older fossils does not rule out a somewhat earlier odontocete radiation. This postulated scenario of rapid cetacean diversification 30–34 Mya may appear unlikely, but some recent studies of marine mammals have shown that morphological differentiation (e.g., of the gray whale) may occur rapidly in conjunction with adaptation to a new ecological niche (Arnason and Gullberg 1994; Arnason et al. 1995). This observation is also supported by the present results in which the close molecular similarity found between the Irrawaddy dolphin and other delphinids contradicts morphological studies that have claimed close affinities between this species and the family Monodontidae.

The evolutionary relationships reported here and the presently proposed dating of cetacean divergencies are incompatible with the conclusions of Milinkovitch et al. (1993) that the odontocete sperm whales and the mysticete family Balaenopteridae (rorquals) had a common ancestor 10–13 Mya. As support for their interpretation, Milinkovitch, Ortí, and Meyer (1993) stated that "This [i.e., the split between sperm whales and Balaenopteridae] is not in disagreement with the palaeontological data because the oldest fossils of balaenopterids are from Late Miocene deposits (5–10 Myr)." These conclusions were rebutted by Arnason and Gullberg (1994), who demonstrated that, relative to other mysticetes, there were no particular sperm whale/rorqual affinities. Milinkovitch, Ortí, and Meyer (1993) also claimed that their analysis involved all major groups of cetaceans, except river dolphins. This is a questionable statement considering that Milinkovitch, Ortí, and Meyer (1993) included only two mysticete species, the fin and humpback whales (both of family Balaenopteridae), and could therefore not make a hypothesis involving three unrepresented families, Balaenidae, Neobalaenidae, and Eschrichtiidae. In a more recent communication, Milinkovitch, Ortí, and Meyer (1995) have reached a similar understanding, stating that "it is conceptually inappropriate to assert relationships between three or more taxa when data from one of them are not included in the analysis." The mysticete paleontological record exceeds by far the 10–13-Mya dating of the evolutionary separation of sperm whales and rorquals proposed by Milinkovitch, Ortí, and Meyer (1993). Therefore, as argued by Arnason and Gullberg (1994), the phylogeny proposed by Milinkovitch, Ortí, and Meyer (1993) implied,

not only odontocete but also mysticete paraphyly. The findings of Milinkovitch, Ortí, and Meyer (1993) should also be considered in the light that they were based on partial rRNA sequences and that analyses of complete 12S rRNA sequences (Douzery 1993) do not resolve the relationship among mysticetes, dolphins, and sperm whales. Milinkovitch et al. in their papers (1993, 1994, 1995) have complemented the proposed sperm whale/rorqual relationships with some nonmolecular data. The validity of the nonmolecular argumentation, notably the echolocation support, was challanged by Ohland, Harley, and Best (1995). The molecular data of Ohland, Harley, and Best (1995), restriction mapping of mtDNA, were consistent with the common understanding of cetacean relationships and did not provide support for the phylogeny proposed by Milinkovitch, Ortí, and Meyer (1993).

In their analysis of the cetacean cytochrome *b* sequences presented by Arnason and Gullberg (1994), Adachi and Hasegawa (1995) showed that the relationship among the three clades available (mysticetes, dolphins, and sperm whales) was sensitive both to sampling and to the choice of outgroup. The present availability of a larger number of cetacean cytochrome *b* sequences, representing all extant cetacean clades, made it possible to examine further the findings of Adachi and Hasegawa. The results showed that by changing either, or both, the cetacean and the artiodactyl representation, and/or by selecting different outgroups, it was possible to produce virtually any tree topology for the most parsimonious relationship among the five cetacean clades recognized in figure 1. The lability of the relationship among these clades suggests that any proposal for sister group relationship among any of the five clades should be expressed with caution unless strongly supported by different data and approaches. Lecointre et al. (1993) have shown that comprehensive species sampling promotes the identification of correct phylogenetic trees. We feel, therefore, that the most parsimonious tree based on the comprehensive species representation of figure 1 carries more credibility than trees produced on the basis of partial sequences and a more restricted number of taxa.

With respect to the labile relationship among different cetacean clades, it is noteworthy that similar results were obtained by both maximum likelihood (ML) analysis (Adachi and Hasegawa 1995) and the present parsimony analysis of CNS. It should be observed, however, that ML does not perform particularly well among the mysticetes, where the topology of the cytochrome *b* tree presented by Adachi (1995) can be evaluated in relation to other, both molecular and nonmolecular, characteristics. Mysticete karyology has been worked out in considerable detail (Arnason 1974, 1982*a*). The general

$2n = 44$ cetacean karyotype is a mysticete characteristic. There is, however, one exception, namely the family Balaenidae, which has 42 chromosomes (Jarrell 1979; Arnason, Purdom, and Jones 1982). The $2n = 42$ balenid karyotype has arisen from the $2n = 44$ karyotype by fusion of two pairs. In the ML tree presented by Adachi (1995), the two extant balenid species are nested among members of the family Balaenopteridae (rorquals). This particular topology is incompatible not only with chromosomal findings, but also with all other paleontological, morphological, and molecular data.

Adachi and Hasegawa (1995) evaluate three cetacean phylogenetic hypotheses, the "Milinkovitch tree," the "traditional tree," and the "Arnason tree." In their paper, Adachi and Hasegawa (1995) credit us (Arnason and Gullberg 1994) with an evolutionary hypothesis showing particular mysticete/dolphin affinities, even though the bootstrap values we reported for these affinities were only 52 and 49, respectively. In response, we must point out that we did not anywhere oppose our findings to the traditional view of cetacean systematics. The reason for this is that, at least in our view, new evolutionary hypotheses should be supported by a more comprehensive representation of taxa than was available at that time.

The most parsimonious cytochrome *b* relationship for artiodactyls and cetaceans is (Camelidae ((Suidae + Tayassuidae) ((Ruminantia (*Hippopotamus*) Cetacea))). Previous mtDNA studies (Arnason et al. 1991; Irwin, Kocher, and Wilson 1991; Graur and Higgins 1994) have provided details of artiodactyl/cetacean affinities and at the same time suggested artiodactyl paraphyly. Recent analyses of cytochrome *b* in a large number of mammalian species, albeit with a limited cetacean representation, have suggested cetacean/hippopotamus affinities (Irwin and Arnason 1994). The present findings, with a much more extensive cetacean representation, are consistent with that result and, at the same time, make the Suiformes (pigs, peccarys, hippopotamuses) paraphyletic. Suiformes paraphyly conforms to other molecular findings that have shown affinities between Hippopotamidae and the Ruminantia (Beintema et al. 1988; Czelusniak et al. 1990; Stanhope et al. 1993). The present character-based results show affinities between hippopotamus and cetaceans and conform to distance analysis of albumin (Sarich 1993). Neither analysis groups hippopotamus with the suids.

The mean conservative nucleotide difference among the five cetacean lineages is 7.1% as compared with 12.6% between cetaceans and artiodactyls. A comparison with an extensive outgroup representation of carnivores suggests that the evolution of cetacean mtDNA is 5%–10% faster than that of artiodactyls (Krettek, Gullberg, and Arnason 1995). If we accept the

figure 30–34 Mya for the cetacean divergence, the different values suggest that artiodactyls and cetaceans had a common ancestor ≈60 Mya. Within the Artiodactyla, the most distant relationships may have only slightly earlier datings, ≈65 Mya. The age of the earliest cetacean paleontological findings, >50 Myr (Gingerich et al. 1994; Thewissen, Hussain, and Arif 1994), may appear old relative to the evolution of the Artiodactyla. The present molecular analysis suggests, however, that the age of the oldest cetacean fossils falls well within the dating of the artiodactyl/cetacean separation.

From the morphological point of view, the now-proposed cetacean cladogenesis, 30–34 Mya, may appear unlikely. In this context it should, however, be kept in mind that both the present and previous results on marine mammals, both cetaceans and pinnipeds (Arnason and Gullberg 1994; Arnason et al. 1995), have shown that morphological differentiation may occur very rapidly in conjunction with adaptation to a new ecological niche. In this light, identification of the probable ancestor of the five extant cetacean lineages will be a challenging undertaking for cetacean paleontology.

Acknowledgments

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