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Evolution of the Common Cetacean Highly Repetitive DNA Component and the Systematic Position of *Orcaella brevirostris*

S. Grétarsdóttir and Ú. Árnason

Department of Molecular Genetics, The Wallenberg Laboratory, University of Lund, Box 7031, S-220 07 Lund, Sweden

Summary. The common cetacean highly repetitive DNA component was analyzed with respect to its evolution and value for establishing phylogenetic relationships. The repeat length of the component, which is tandemly organized, is ≈1750 bp in all cetaceans except the delphinids, in which the repeat length is ≈1580 bp.

The evolution of the component was studied after sequencing the component in different odontocetes representing the Delphinidae (delphinids), Monodontidae (narwhals), and Ziphiidae (beaked whales). The evolution of this component is very slow, and comparisons showed that sequence divergence among species corresponds closely to their generally accepted phylogenetic relationships and that the component evolves in a concerted manner.

The phylogenetic information obtained in this study identified the Irrawaddy dolphin (*Orcaella brevirostris*) as a delphinid and did not support a close relationship of this species with the Monodontidae.

Key words: Highly repetitive DNA — Cetacea — Evolutionary rates — Molecular phylogeny

Introduction

Tandemly organized highly repetitive DNA (satellite DNA) has been thought to evolve rapidly. In mammals, this idea has been primarily supported by extensive studies on centromeric satellite DNAs (e.g., Miklos 1985; Dod et al. 1989; Way and Willard 1989).

Offprint requests to: S. Grétarsdóttir

A characteristic tandemly organized highly repetitive DNA (hrDNA) component occurs in all cetaceans, both odontocetes (toothed whales) and mysticetes (whalebone whales) (Árnason et al. 1984). This component is located in most interstitial and terminal C-bands, and the repeat length is about 1750 bp in all cetacean families except the Delphinidae, in which the full length component has been largely replaced by a 1580-bp variety resulting from a deletion of 170 bp (Widegren et al. 1985; Árnason 1987; Árnason and Widegren 1989). The common cetacean component has several characteristics; the repeat unit is unusually long compared with other known hrDNA fragments, it contains no internal linear repetition (Widegren et al. 1985), and its fragment length (apart from the Delphinidae members) and basic sequence composition has been maintained during the evolution of the order Cetacea. Odontocetes and mysticetes separated evolutionarily ≥40 million years (Myr) ago (Barnes et al. 1985), and the similarities that have been maintained in the composition of the component in the two suborders show that its evolution is very slow.

The occurrence of a common component in all cetaceans allows different levels of comparison, from within families to between suborders. The present study addressed the question of concerted evolution in this common cetacean component. The material studied was from the Irrawaddy dolphin (*Orcaella brevirostris*), the killer whale (*Orcinus orca*), Heaviside's dolphin (*Cephalorhyncus heavisidii*), the beluga (*Delphinapterus leucas*), and Baird's beaked whale (*Berardius bairdii*). Baird's beaked whale is a member of the superfamily Ziphioidea, whereas the rest of the species belong to the superfamily Delphinoidea. Comparisons were made between these two odontocete superfamilies, and the systematic position of the Irrawaddy dolphin was investigated.

Materials and Methods

Source of Material. The *O. brevirostris* samples were collected in Australia by John Bannister, and the DNA was provided by James W. Clayton and W.R. Lillie. The samples of *C. heavisidii* were collected in South Africa by Peter B. Best. The *D. leucas* samples were collected by Claire Cirone on Baffin Island, and the samples of *B. bairdii* were collected in Japan by James Mead. The *O. orca* sample originated from Iceland. Total genomic DNA was extracted from solid tissue (liver and/or spleen).

Cloning. Monomeric repeats of the common cetacean component were obtained by electroelution of DNA fragments from preparative agarose gels after SacI digestion. The isolated fragments were cloned in pUC19 and transformed into *Escherichia coli* strain JM101. Positive clones were selected by colony hybridization (according to Sambrook et al. 1989) using a cloned hrDNA component from the bowhead whale (*Balaena mysticetus*) as a labeled probe.

Sequencing. The *O. orca* hrDNA component was sequenced using double-stranded dideoxy sequencing with T7-polymerase (Tabor and Richardson 1987). Positive clones from *C. heavisidii, O. brevirostris, D. leucas,* and *B. bairdii* were subcloned in M13 for single-stranded dideoxy sequencing. The sequencing was performed in both directions using both universal primers and different internal primers. Three different repeats from one individual of each species (five repeats in *B. bairdii*) were sequenced, and a consensus sequence was determined according to the majority vote at each position of the repeats. In positions where majority was not obtained for a consensus, the IUB/GCG sequence symbols were used (e.g., H instead of A, C, and T).

Sequence Analyses. DNA sequences were analyzed and compared using computer programs from the University of Wisconsin Genetics Computer Group, GCG (Deveraux et al. 1984). The BESTFIT program (from GCG), which uses the "local homology" algorithm of Smith and Waterman (1981) was used to obtain alignment in pairwise comparisons and to estimate the percent similarity. Phylogenetic trees were constructed from DNA sequence data using the programs DNAPARS from PHYLIP 3.3 (Felsenstein 1990) and TreeAlign (Hein 1990). A consensus tree was constructed after 50 bootstrap replications using the program DNABOOT (Felsenstein 1985, 1990). The method of Strachan et al. (1985) was applied to analyze the patterns of variation at each nucleotide position among clones in the pairwise comparisons: *O. orca/O. brevirostris, O. orca/D. leucas,* and *O. orca/B. bairdii.* With this method, the spread and fixation of variant repeats can be analyzed. The variation at each nucleotide position between clones of both species is classified into six different categories (classes 1–6).

Class 1: completely homogeneous positions in all clones of both species in pairwise comparisons (species A: N_1, species B: N_1; where N = G, A, T, or C). This class thus represents the absence of mutation in the ancestor base (N_1) shared by both species.

Class 2: the minority of clones have a new mutation (N_2) at a position, whereas the majority of clones remain homogeneous for the ancestor base (species A: N_1 only, species B: $N_1 > N_2$).

Class 3: positions where the ancestor bases and the mutations are in equal frequencies (species A: N_1 only, species B: $N_1 = N_2$).

Class 4: positions where one species is homogeneous for the ancestor base but a mutation has replaced this base in the majority of clones in the other species (species A: N_1 only, species B: $N_2 > N_1$).

Class 5: positions where the two species are homogeneous for different bases, the classical observation of concerted evolution (species A: N_1 only, species B: N_2 only).

Class 6: situations including all subsequent mutations (species A: N_1 only, species B: $N_2 > N_3$).

Table 1. Lengths of highly repetitive DNA sequence in species of cetaceans of superfamily Delphinoidea

Species[a]	Sequence length (bp)	
	Actual[b]	Approximate[c]
Family Monodontidae		
Subfamily Delphinapterinae		
Delphinapterus leucas	1742	1750
Subfamily Monodontinae		
Monodon monoceros	1743	1750
Family Phocoenidae		
Subfamily Phocoeninae		
Phocoena phocoena	1744	1750
Family Delphinidae		
Subfamily Delphininae		
Lagenorhyncus albirostris		1580
Delphinus delphis		1580
Tursiops truncatus		1580
Stenella attenuata		1580
Stenella longirostris		1580
Subfamily Cephalorhyncinae		
Cephalorhyncus heavisidii	1579	1580
Subfamily Globicephalinae		
Orcinus orca	1573	1580
Globicephala melaena		1580
Globicephala macrorhynchus		1580
Subfamily Orcaellinae		
Orcaella brevirostris	1583	1580

[a] Relationships and designations are according to Heyning (1989)
[b] Actual consensus component length based on DNA sequencing
[c] Approximation based on restriction fragment analysis (Árnason et al. 1984; Árnason, unpublished)

Results

The approximate sequence length of the common cetacean component in 13 species of the superfamily Delphinoidea has been determined by restriction fragment analysis (Árnason et al. 1984; Árnason, unpublished). Table 1 lists those species of the Delphinoidea in which the presence of this component has been documented. The ≈1750-bp hrDNA component is present in the representative of the Phocoenidae, *Phocoena phocoena* (the harbour porpoise) and in *D. leucas* and *Monodon monoceros* (narwhal) of the Monodontidae. All members of the Delphinidae that have been examined have the shorter hrDNA component of ≈1580 bp. *Orcaella brevirostris* also has a fragment length of ≈1580 bp as in the Delphinidae, thereby separating this species from *D. leucas* and *M. monoceros.*

Nucleotide sequences of the hrDNA components in *O. brevirostris, O. orca, C. heavisidii, D. leucas,* and *B. bairdii* were determined. The sequences of

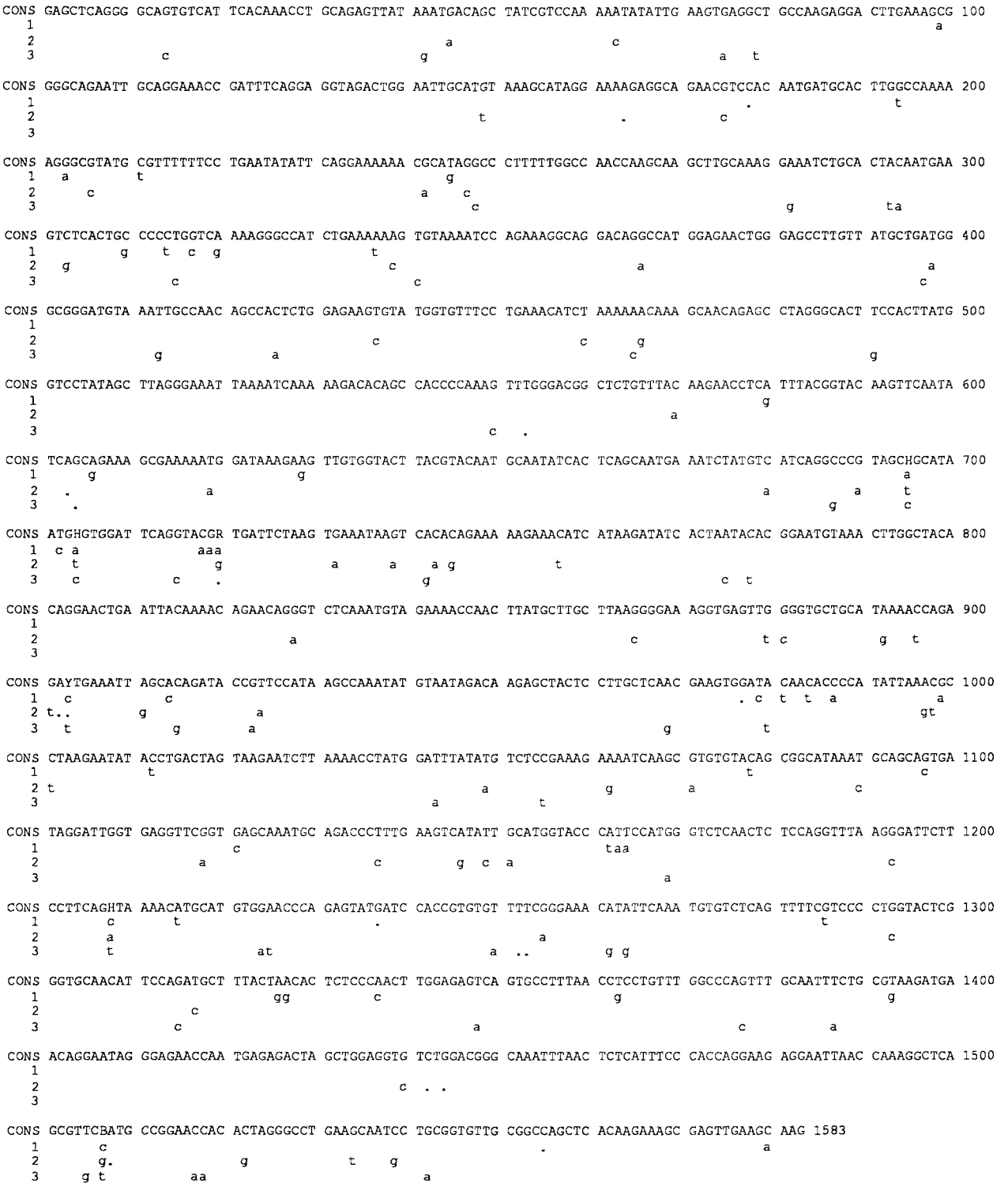

Fig. 1. Consensus sequence and sequences of three clones of the common highly repetitive DNA repeat of *Orcaella brevirostris*. Deviations from the consensus sequence are shown in lowercase letters. Dots indicate missing bases.

three repeats and the consensus sequence of *O. brevirostris* are presented in Fig. 1. The sequences of individual repeats for the other species are not presented, but their lengths together with the consensus length and average sequence similarity are shown in Table 2. In Fig. 2, the different consensus sequences are shown aligned to the longest sequence, that of *D. leucas*. A characteristic of the common cetacean component is a 72-bp inverted repeat sequence with high intrastrand complementarity (positions 190–262 in Fig. 2). This portion is highly conserved in all cetacean species so far examined (Widegren et al. 1985; Árnason and Widegren 1989).

We analyzed the spread and fixation of variant repeats in pairwise comparisons between *O. orca* and three related species; *O. brevirostris, D. leucas,*

Table 2. Lengths of individual sequenced DNA repeats and the consensus sequences in several odontocete cetaceans

Species	Length of repeats (bp)	Consensus length[a] (bp)	Average similarity among repeats (%)[b]
Orcaella brevirostris	1581 1577 1579	1583	94.2
Orcinus orca	1569 1568 1567	1573	94.0
Cephalorhyncus heavisidii	1578 1581 1578	1579	95.5
Delphinapterus leucas	1740 1745 1738	1742	92.2
Berardius bairdii	1744 1740 1740 1746 1743	1740	96.2

[a] Based on majority vote

[b] Individual repeats were compared using the BESTFIT program (GCG) and an average similarity (%) within each species calculated

Table 3. Classification of distribution of DNA mutations (%) at individual nucleotide position in pairwise comparisons between *Orcinus orca* and three other cetacean species

Class[a]	*Orcinus orca* versus		
	Orcaella brevirostris	*Delphinapterus leucas*	*Berardius bairdii*
1	82.9	78.7	71.1
2	14.1	13.1	9.6
3	—	—	—
4	0.6	1.9	3.0
5	0.2	3.6	12.4
6	1.1	1.4	1.6

[a] See Materials and Methods for explanation of the different classes

Table 4. Similarity matrix (%) of consensus nucleotide sequence of the highly repetitive DNA components from five cetacean species

	Cephalorhyncus heavisidii	*Orcinus orca*	*Delphinapterus leucas*	*Berardius bairdii*
Orcaella brevirostris	96.0	98.1	93.7	81.6
Cephalorhyncus heavisidii		96.7	92.9	81.3
Orcinus orca			93.7	81.5
Delphinapterus leucas				81.0

Sequence comparisons were performed with the BESTFIT program (GCG)

and *B. bairdii*. All available clones from these species were compared, and each nucleotide position was classified according to the method of Strachan et al. (1985). This analysis reveals different stages of transition in the fixation of randomly produced variant repeats. More than 98% of all nucleotide positions in the comparisons could be classified using this system. The distribution of mutations in these species is presented in Table 3. The majority of nucleotide positions are homogeneous in all comparisons (class 1), i.e., no mutation has occurred in any of the clones. The percentage of nucleotide positions where different bases have been fixed in the two species (class 5 plus 6) is 1.3% for *O. orca/O. brevirostris*, 5% for *O. orca/D. leucas*, and 14% for *O. orca/B. bairdii*.

Comparison of the consensus sequences (Table 4) using the BESTFIT program of the GCG package showed that the highest degree of similarity was between the sequences of *O. brevirostris* and *O. orca* (98.1%), whereas the level of similarity between *O. brevirostris* and *D. leucas* was somewhat less (93.7%). *Berardius bairdii* represents a distinct outgroup in this comparison with almost the same degree of similarity with *D. leucas, C. heavisidii, O. orca,* and *O. brevirostris* (81.0, 81.3, 81.5, and 81.6%, respectively). To evaluate the evolutionary relationships among the five species, parsimony analysis was carried out on the consensus sequences. The consensus sequences were aligned (Fig. 2), and parsimony analysis was performed with *B. bairdii* designated as the outgroup (Felsenstein 1990). The most parsimonious tree is shown in Fig. 3a.

To find the confidence interval of this phylogeny the sequence data was resampled with the bootstrap method (Felsenstein 1985, 1990). The consensus tree resulting from 50 bootstrap trials is identical to the parsimony tree, and the relationship presented in Fig. 3a was identified in more than 95% of the trials. The grouping of *D. leucas, C. heavisidii, O. brevirostris,* and *O. orca* (node A) and *C. heavisidii, O. orca,* and *O. brevirostris* (node B) was identified in 100% of the bootstrap trials, and the relationship between *O. orca* and *O. brevirostris* (node C) was identified in 97% of the trials.

Another analysis of the relationship of the five species was performed by using a multiple sequence alignment program (Hein 1990) that constructs trees using a combination of distance matrix and approximate parsimony methods (Fig. 3b). In the parsimony tree and the TreeAlign tree, *O. brevirostris*

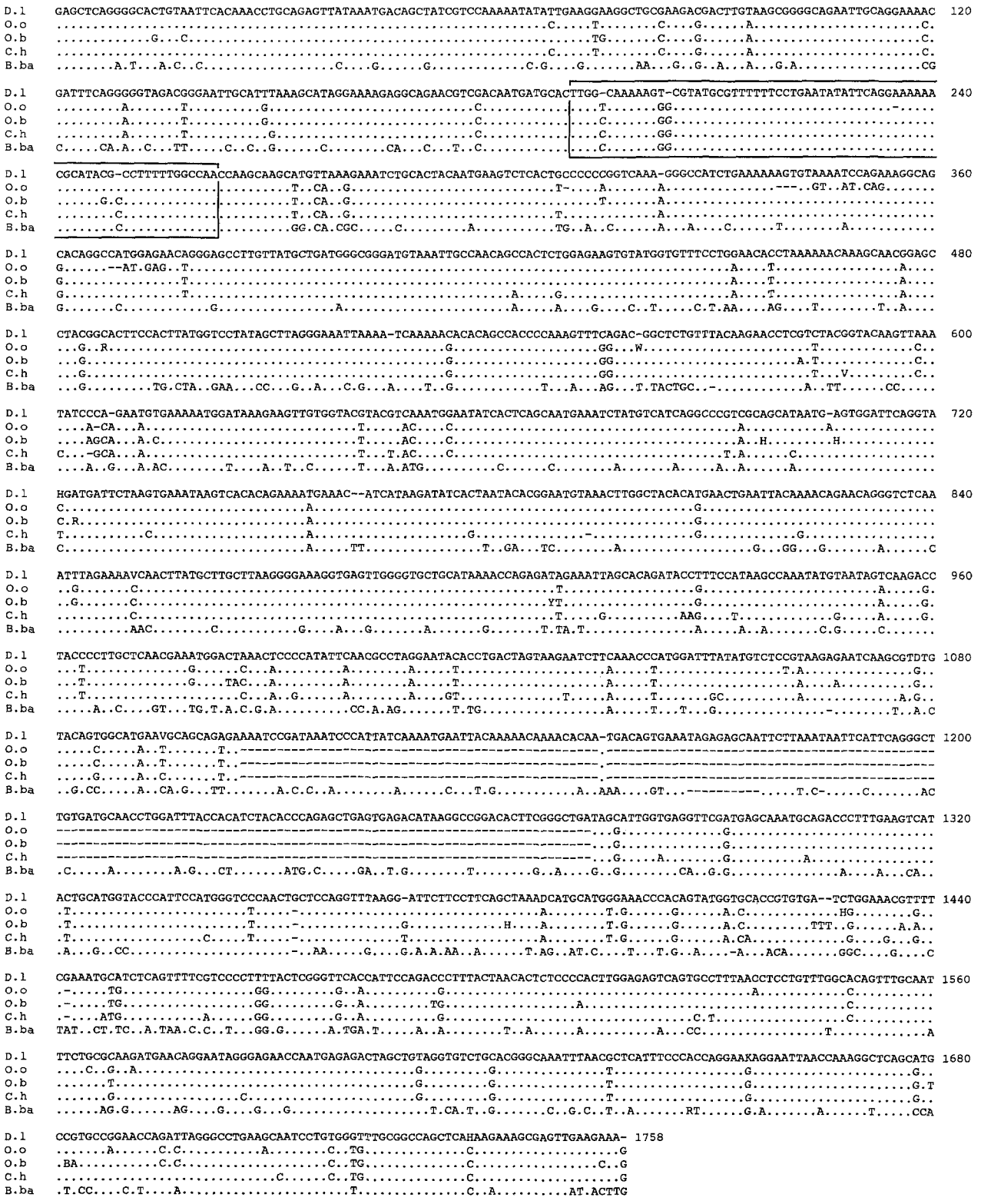

Fig. 2. Alignment of the highly repetitive DNA consensus sequences of *Delphinapterus leucas* (D.l.), *Orcinus orca* (O.o.), *Orcaella brevirostris* (O.b.), *Cephalorhyncus heavisidii* (C.h.), and *Berardius bairdii* (B.ba.). The complete DNA sequence is presented for *D. leucas* (including gaps inserted for the consensus alignment); dissimilarities in the other sequences are shown with capital letters. The IUB/GCG symbols used are W = A/T, H = A/C/T, R = A/G, V = A/C/G, Y = C/T, D = A/G/T, and K = G/T. Gaps/deletions are shown as hyphens. A dot indicates an identical base as in *D. leucas* sequence. The large gap in *O. orca, C. heavisidii,* and *O. brevirostris* from positions 1106 to 1277 represents the ≈170-bp deletion in the common cetacean 1750-bp component that characterizes the 1580-bp delphinid component. The enclosed sequence from positions 190 to 262 is a 72-bp region with a conspicuous intrastrand complementarity.

groups with the other Delphinidae members, but the trees show different branching order of *O. orca, O. brevirostris,* and *C. heavisidii.* In the parsimony tree (Fig. 3a), *O. orca* and *O. brevirostris* are joined, whereas the TreeAlign tree (Fig. 3b) joins *O. orca* with *C. heavisidii.* However, the branching order of *B. bairdii* and *D. leucas* is identical in both trees.

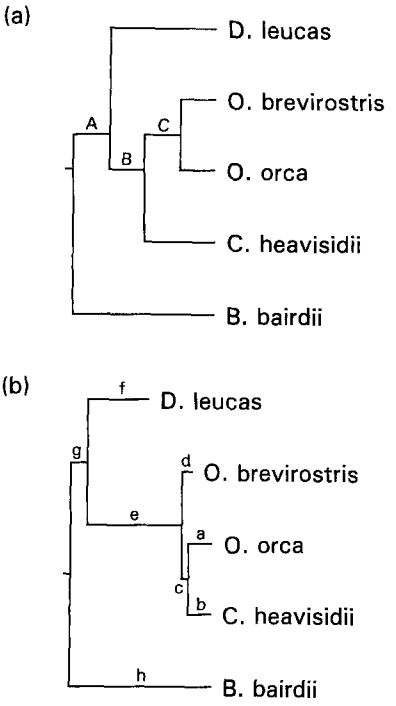

Fig. 3. Phylogenetic relationship of *Cephalorhyncus heavisidii, Orcaella brevirostris, Orcinus orca, Delphinapterus leucas,* and *Berardius bairdii.* **a** Tree based upon unrooted parsimony analysis of the nucleotide sequence of the highly repetitive (hr)DNA component. The *B. bairdii* sequence was chosen as an outgroup. Nodes A and B were identified in 100% and node C in 97% of the trials performed by the bootstrap method in PHYLIP 3.3 (Felsenstein 1985). Branch lengths are not related to taxonomic distance. **b** Tree based on distance matrix and parsimony analysis of the hrDNA component of *C. heavisidii, O. brevirostris, O. orca, D. leucas,* and *B. bairdii.* Branch lengths represent changes estimated by the TreeAlign program, and the tree is rooted assuming a molecular clock, which might not be justified (Hein 1990). Relative lengths of the branches: a = 168, b = 170, c = 44, d = 74, e = 654, f = 423, g = 111, h = 979.

Discussion

Tandemly organized hrDNA sequences (DNA satellites) usually show marked heterogeneity both with respect to fragment length and composition (Miklos 1985). Because of the rapid evolution of these components, their value in phylogenetic analysis is limited in most cases, as the distribution of each component is usually restricted to the level of species or genus.

The evolution of satellite DNA has been a subject of considerable theoretical and analytical treatment with particular emphasis on the apparent concerted evolution of these components (e.g., Dover 1982; Willard and Way 1987; Dod et al. 1989; Way and Willard 1989). The essence of concerted evolution is that each individual member of a repeat family does not evolve independently of other members of the same family. The members of a satellite DNA family are therefore very similar within a species, whereas repeats from different species can be distinctly different, even among closely related species.

The common cetacean component occurs in all cetacean families (Árnason 1982; Árnason et al. 1984). The presence of the component in both odontocetes and mysticetes dates the age of the component to more than 40 Myr, i.e., the time of the evolutionary separation of the two cetacean suborders (Barnes et al. 1985). The component is characterized by a striking conservation, both with respect to its fragment length and its sequence composition. The component constitutes a large portion of the cetacean genomes, $\geq 15\%$ in *O. orca,* in which the copy number has been estimated at $4–5 \times 10^5$ (Widegren et al. 1985). The chromosomal localization of the component is known; it occurs primarily in interstitial and terminal chromosome positions (Widegren et al. 1985; Árnason 1987; Árnason and Widegren 1989).

This study underlines the slow evolution of the common cetacean component and provides details that support the occurrence of concerted evolution in this satellite. The analyses show that individual repeats of the component have a higher degree of conformity within a species than between different species. However, when consensus sequences from closely related species are compared, the conformity of the different consensus sequences can exceed that of individual repeats within a species. Thus, the average identity between the repeats of *O. orca* is 94.2% (Table 2), but the identity between the consensus sequences of *O. orca* and *C. heavisidii* is 96.7% and between *O. orca* and *O. brevirostris* is 98.1% (Table 4). These findings seem to contradict the concept of concerted evolution, but when the distribution of variant components is compared in the different species (Table 3), the evolutionary pattern of the component emerges. This comparison reveals all the expected transition stages from no replacement (classes 2, 3, and 4) to complete replacement as fixation of variants (classes 5 and 6). In the most closely related species, *O. orca* and *O. brevirostris,* 14.6% of the nucleotide positions fall into the intermediate classes and only 1.3% into the category that represents the classical manifestation of concerted evolution, i.e., when each species is homogeneous for a different base. At increasing evolutionary distance, the spread of variant repeats becomes more pronounced, 5% in *O. orca* versus *D. leucas* and 14% in *O. orca* versus *B. bairdii.* These

figures can be compared with odontocete paleontological data, which records the oldest delphinid fossils about mid-Miocene. However, the major delphinid radiation occurred later, and the oldest fossils of the modern delphinid genera are from late Pliocene (Heyning, personal communication). The Monodontidae and Delphinidae separated about 11 Myr ago, and the fossil record of the Ziphiidae goes back to at least mid-Miocene, about 16 Myr ago (Barnes et al. 1985). Our findings suggest that the common cetacean component evolves at an evolutionary rate that is reasonably well related to time. However, this rate appears to be considerably slower than that of other mammalian satellite DNAs so far studied.

In mysticetes, three different DNA satellites have been identified. One is the common cetacean component, the other two are the heavy and light balaenopterid satellites (Árnason et al. 1978, 1988). The heavy satellite, which is located in telomeric chromosome positions, evolves at a rate that is similar or even slower than that of the common cetacean component (unpublished). The light satellite, which occurs in centromeric regions in telocentric chromosomes (Árnason et al. 1978; Árnason and Widegren 1989), has a strikingly differentiated pattern that is species specific (Árnason and Best 1991). Thus, the light satellite appears to evolve at a much higher rate than the other two components.

Nonhomologous chromosome exchanges may occur more readily between telocentric than between metacentric chromosomes, which may promote the spreading of variant repeats and subsequent homogenization within a repeat cluster (Dod et al. 1989). This hypothesis is highly plausible, considering the different rate of evolution of the mysticete DNA satellites, although other factors such as length or number of the repeat units may also affect the evolutionary rate of DNA satellites. Studies on changes in array length (the number of repeat units) in minisatellites (Jeffreys et al. 1988) have shown that regions composed of short repeat units change very rapidly (possibly by unequal crossing-over), and computer simulations on tandemly organized sequences have shown that short repeats undergo unequal crossing-over more frequently than do longer repeats (Stephan 1989).

The common cetacean component has provided molecular evidence for a monophyletic origin of the Cetacea (Árnason et al. 1984), and different mysticete relationships have been assessed on the basis of the occurrence and organization of the mysticete DNA satellites (Árnason and Best 1991). We used this component to investigate the relationship between *O. brevirostris* and the representatives of the Delphinidae and Monodontidae, using *B. bairdii* as an outgroup.

Several morphologic studies have dealt with relationships within and between the families of the Delphinoidea (Fraser and Purves 1960; Nishiwaki 1963, 1964; Fraser 1966; Ness 1967; Mitchell 1970; Kasuya 1973; Mead 1975; Barnes 1978, 1984; Heyning 1989). Kasuya (1973) argued that *Delphinapterus* and *Orcaella* should comprise a new family, the Delphinapteridae. Barnes (1984) shared the opinion that the genus *Orcaella* should be removed from the family Delphinidae and suggested that it should be included as the subfamily Orcaellinae in the family Monodontidae, together with the subfamilies Delphinapterinae and Monodontinae. In another study, Heyning (1989) argued that several characteristics in *Orcaella* that are synapomorphies for the delphinid/phocoenid clade are not found in *Delphinapterus* and *Monodon* and therefore concluded that *Orcaella* should be retained in the Delphinidae until more conclusive evidence was presented in favor of its exclusion from that family.

The systematic position of *Orcaella* was recently analyzed using serum albumin immunology and enzyme electrophoresis (Lint et al. 1990). This study showed a close relationship between *M. monoceros* and *D. leucas,* and grouped *O. brevirostris* with the delphinids. These findings closely parallelled the enzyme electrophoresis data of Shimura and Numachi (1987), and both data sets supported the same relative phylogenetic positions of the families Phocoenidae, Ziphiidae, and Delphinidae. Among these three families, the Phocoenidae and the Ziphiidae were more closely related. Lint et al. (1990) also found that the Monodontidae occupied a phylogenetic position intermediate between Ziphiidae and Phocoenidae.

Our analysis of the common cetacean component identified *Orcaella* as a delphinid species based on its possession of the typical delphinid ≈1580-bp variety of the component. The comparison of the composition of the component and the phylogenetic analyses (Fig. 3a and b) also placed *Orcaella* among the delphinids. The relationship between *Orcaella, C. heavisidii,* and *O. orca* was, however, not unequivocally resolved in the analysis. The parsimony tree (Fig. 3a) associates *O. orca* and *O. brevirostris* to the exclusion of *C. heavisidii,* but in the TreeAlign tree (Fig. 3b) the situation is reversed. The hrDNA sequences from these species are very similar when compared using the alignment programs BESTFIT (Table 3) and TreeAlign (*O. brevirostris* vs. *O. orca* = 98%, *O. orca* vs. *C. heavisidii* = 96%, and *O. brevirostris* vs. *C. heavisidii* = 95%), and in both programs, the highest degree of similarity is between *O. orca* and *O. brevirostris.*

In our analyses, the Ziphiidae (beaked whales) were represented by only one species, *B. bairdii.* The DNA sequence data analysis separated *B. bairdii* distinctly from the four delphinoid species, which agrees with the classical phylogenetic view but not

with the immunology and protein electrophoresis data (Lint et al. 1990).

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