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Morphology, Molecules, and the Phylogenetics of Cetaceans

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Abstract.—Recent phylogenetic analyses of cetacean relationships based on DNA sequence data have challenged the traditional view that baleen whales (Mysticeti) and toothed whales (Odontoceti) are each monophyletic, arguing instead that baleen whales are the sister group of the odontocete family Physeteridae (sperm whales). We reexamined this issue in light of a morphological data set composed of 207 characters and molecular data sets of published 12S, 16S, and cytochrome *b* mitochondrial DNA sequences. We reach four primary conclusions: (1) Our morphological data set strongly supports the traditional view of odontocete monophyly; (2) the unrooted molecular and morphological trees are very similar, and most of the conflict results from alternative rooting positions; (3) the rooting position of the molecular tree is sensitive to choice of artiodactyl outgroup taxa and the treatment of two small but ambiguously aligned regions of the 12S and 16S sequences, whereas the morphological root is strongly supported; and (4) combined analyses of the morphological and molecular data provide a well-supported phylogenetic estimate consistent with that based on the morphological data alone (and the traditional view of toothed-whale monophyly) but with increased bootstrap support at nearly every node of the tree. [Cetacea, DNA sequences, likelihood-ratio test, molecular clock, morphology, Mysticeti, Odontoceti, partition-homogeneity test, phylogeny, Templeton test.]

Extant cetaceans traditionally have been placed in two suborders, Odontoceti (toothed whales) and Mysticeti (baleen whales), both of which were thought to be monophyletic on the basis of numerous morphological, physiological, and behavioral characteristics (Gray, 1863; Flower, 1883; Kellogg, 1928; Van Valen, 1968; Barnes and Mitchell, 1978; Fordyce, 1980, 1992; Muizon, 1984; Heyning, 1989; Heyning and Mead, 1990; Arnason and Gullberg, 1996). Recent phylogenetic analyses employing DNA sequence data have suggested that this long-held view of whale relationships is incorrect and that sperm whales (Physeteridae) are more closely related to baleen whales than they are to other odontocetes (Milinkovitch et al., 1993, 1994, 1996; Milinkovitch, 1995; Smith et al., 1996; but see Arnason and Gullberg, 1994, 1996, for conflicting molecular results). Milinkovitch et al. (1993, 1994) and Milinkovitch (1995) have suggested taxonomic modifications and reinterpretation of morphological characters in the context of the molecular tree, yet we believe that this controversial phylogenetic hypothesis requires further scrutiny. In particular, we believe that morphological data should be considered in the phylogenetic analysis, rather than reinterpreted in the context of the molecular hypothesis. With this approach, we assess empirically whether the molecular and morphological data are in conflict and whether the Milinkovitch et al. (1993, 1994) hypothesis is supported by a larger data set composed of molecular and morphological characters.

Several recent papers addressing cetacean phylogeny, including Milinkovitch et al. (1993, 1994), Milinkovitch (1995), and Arnason and Gullberg (1996), have employed a molecular clock as a means of estimating divergence times for whale lineages, particularly the timing of divergence between sperm and baleen whales. Fossils dating back 30–38 million years have been identified as toothed mysticetes, and both toothed and baleen-bearing mysticetes were said to be present in the late Oligocene roughly 30 million years ago (Fordyce, 1989, 1992). Although the initial molecular clock-based time-since-divergence estimate of 10–13 mil-

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lion years (Milinkovitch et al., 1993) for Mysticeti and Physeteridae has since been adjusted to 18–19 million years (Milinkovitch, 1995), there remains substantial disagreement between the paleontological evidence and the molecular clock estimate of time since divergence. Molecular clock models require many assumptions, some of which may be quite unrealistic (Hillis et al., 1996). We investigated the appropriateness of the molecular clock assumption for the available 12S, 16S, and cytochrome *b* sequence data in two ways. We tested the assumption that nucleotide substitutions have occurred in a clock-like manner within the cetacean lineage using a likelihood-ratio test. We also calculated minimum confidence intervals for estimates of time since divergence for cetaceans assuming a perfect molecular clock.

Materials and Methods

Morphological Data

We compiled a data set composed of 207 morphological characters drawn from osteology and soft-tissue anatomy for 67 extant species of cetaceans, one composite archaeocete taxon, and five artiodactyl outgroup taxa for which 12S, 16S, and cytochrome *b* mitochondrial DNA sequence data also are available (Appendices 1–3). The ingroup includes representatives of each of the 33 extant genera of odontocetes as well as the three extant families of mysticetes. The archaeocete terminal taxon represents a composite of three late Eocene fossil species (*Basilosaurus cetoides, Zygorhiza kochii, Durodon osiris*), all of which are assumed to predate branching events among extant whales on the basis of character states not seen in extant cetaceans, such as the presence of pelvic limbs (Gingerich et al., 1990) and the absence of telescoping of the skull (Miller, 1923). We are not suggesting that archaeocetes form a natural group and it is not our goal to elucidate relationships between archaeocetes and extant cetaceans. Rather, the inclusion of the composite archaeocete taxon serves to polarize a number of character state transformations that differ between odontocetes and mysticetes but cannot be scored for extant artiodactyls.

Milinkovitch (1995) argued that most of the morphological characters recruited as synapomorphies for Odontoceti are likely to be nonindependent because they seem to be functionally correlated with echolocation. Although there are many putative odontocete synapomorphies that clearly are not related to echolocation, we nevertheless see lack of character independence as an important potential problem for the morphological data and have carefully examined our character set in light of this issue. We have found that many of the characters suspected to be functionally related to echolocation are not distributed among all odontocetes, although all odontocetes are believed to use echolocation (Ketten, 1992; Cranford et al., 1996). In such cases, there is no evidence supporting the contention that the morphological feature in question is required for echolocation, and we therefore treat the morphological feature as an independent character. Our view is that characters should not be excluded from consideration unless there is evidence that a change in one character requires a compensatory change in another. Characters that were judged to be potentially nonindependent on these grounds were excluded from our analysis. Examples of excluded characters include number of blowholes (nonindependent with respect to character 1516 describing the anatomy of the nasal passages), presence or absence of facial asymmetry (nonindependent with respect to characters 1522, 1545, and 1548 describing independent modifications of the nasal plug, vestibular nasal sac, and inferior vestibule, respectively), and development of the cranial vertex (nonindependent with respect to characters 1416, 1420, and 1421 describing presence or absence of crests on the premaxilla and maxillae).

DNA Sequence Data

We obtained from GenBank the 12S, 16S, and cytochrome *b* mitochondrial DNA sequence data used by Milinkovitch et al. (1994). Sequence data for these gene regions are available for 21 cetacean species and 5 artiodactyl outgroup species

(GenBank accession numbers D32189, M55539, M55540, U13079–146, X56286). We wanted our analyses to be directly comparable to those of Milinkovitch et al. (1994). Although we agree with most of the Milinkovitch et al. (1994) protocols, there were three adjustments that we thought would improve the analysis. Therefore, we employed two sets of procedures in our reanalyses of the DNA sequence data. In one set of analyses, we followed the assumptions of Milinkovitch et al. (1994) including their alignment, choice of outgroup taxa (*Bos taurus, Tayassua tajacu, Camelus dromedarius*), and character weighting strategy (transversions weighted three times greater than transitions; indels coded as single transversions with overlapping gaps of different length treated as separate character states; for cytochrome *b,* transitions not considered at the third position of all codons or at the first position of leucine codons). The second set of analyses was based on assumptions that differed only in the exclusion of two ambiguously aligned regions of the 12S and 16S sequences together with their corresponding gap characters (for justification, see later discussion), our inclusion of two additional species of artiodactyl outgroup taxa (*Antilocapra americana, Tragulus napu*), and our adjustment of the alignment of one small gap in the 16S sequence to reconcile its positional homology with constraints imposed by secondary structure of the ribosomal RNA (Gutell, 1994; Kjer, 1995; Hickson et al., 1996). We must note, however, that our inclusion of *A. americana* and *T. napu* required that we make assumptions about sequence alignment that should not be attributed to Milinkovitch et al. (1993, 1994). We will hereinafter refer to the first treatment of the sequence data as the ''Milinkovitch'' sequence data and the second treatment as the ''modified'' sequence data.

Partition-Homogeneity Tests

We performed partition-homogeneity tests (Farris et al., 1995) to assess whether the morphological and molecular data sets are significantly incongruent. We performed these tests to evaluate the presence and/or extent of incongruence between the morphological and molecular data sets and not as a threshold indicator of whether combined-data analyses should be conducted. We acknowledge the conclusions of Bull et al. (1993) that data-set incongruence may indicate that the underlying characters in the data partitions evolved under different models of evolution (which may render a combined-data analysis misleading). However, we do not believe that data-set incongruence should preclude combined-data analysis. Rather, we suggest that a full exploration of the data, whether or not incongruence is detected, should include both individual and combined analyses, but caution should be exercised when interpreting combined-data trees based on data sets found to be incongruent.

The partition-homogeneity test compares the sum of the tree lengths of the data partitions (in this case the molecular data set tree length + the morphological data set tree length) with a null distribution generated by randomly allocating characters from the original partitions into equivalent-sized partitions and then measuring their combined tree lengths. Each of our applications of the test was based on 100 replicate data sets. Because transitions and transversions are differentially weighted in the molecular data sets (transversions weighted three times greater than transitions), the partition-homogeneity test requires a subjective weighting decision for the morphological characters. Two obvious options are to assign weights equivalent with transitions (weight = 1) or transversions (weight = 3), and we chose to perform separate analyses under each set of assumptions. We therefore performed four partition-homogeneity tests, comparing both weighting treatments of the morphological data with our two treatments of the molecular data (modified and Milinkovitch sequence data).

Outgroup Sampling

Recent analyses based on a more limited data set (cytochrome *b* only) suggest that

the root of the molecular tree is sensitive to choice of artiodactyl outgroup taxa (Adachi and Hasegawa, 1995; Arnason and Gullberg, 1996; Milinkovitch et al., 1996). For this reason, we obtained the DNA sequence data for two additional artiodactyl species (*Antilocapra americana, Tragulus napu*) in addition to the three artiodactyl outgroup taxa (*Bos taurus, Tayassua tajacu, Camelus dromedarius*) included by Milinkovitch et al. (1994). These five species (representing five separate families and the three suborders of extant artiodactyls) are the only artiodactyls for which the relevant 12S, 16S, and cytochrome *b* sequence data were available in Genbank at the time of our analysis. To test the sensitivity of the molecular and morphological rooting positions to outgroup taxon sampling, we analyzed the modified DNA sequence and morphological data sets with each of the 31 possible combinations of the five outgroup species. Using the same procedure, we assessed the sensitivity of the root with the Milinkovitch data by performing analyses with each of the seven possible combinations of their three outgroup species.

Gap Treatment

Positional homology within 12S and 16S ribosomal sequences can be difficult to assess, particularly in unpaired regions of the sequence, which may not be constrained by structural interactions with other portions of the sequence (Kjer, 1995; Hickson et al., 1996). The 12S and 16S sequences used here each contain one region of particularly ambiguous alignment, both of which correspond to loop regions in the secondary structure of the ribosomal subunits. Milinkovitch et al. (1993, 1994) applied differential weighting to these gap characters such that they were weighted equivalent to transversions (three times greater than transitions). Although each of these regions is relatively small (12S region = 33 base pairs, 16S region = 20 base pairs), this weighting protocol suggests that these small segments of sequence may have a large impact on the phylogenetic analysis. We tested the sensitivity of the molecular data to alternative alignments of these gap regions as well as to their exclusion from the analysis. Alternative alignments for the gap regions were obtained using the MALIGN (version 1.91) alignment software (Wheeler and Gladstein, 1993). The regions of interest, together with unambiguously alignable short buffer regions on either side of the gap region, were excised from the complete ''Milinkovitch'' data matrix and aligned with gap penalties ranging from one through five. These realigned fragments were then reincorporated into the Milinkovitch data set for analysis. Although we are not convinced that any of these alignments are superior to the original alignment of Milinkovitch et al. (1994), our goal was to provide alternative alignments that are both objective and realistic. Therefore, the alignments provided by MALIGN were adjusted only to account for secondary structure when structural conflicts were observed.

Phylogenetic Analyses

Phylogenetic analyses were performed using test versions of PAUP* (4.0d45, 4.0d53, 4.0d54, 4.0d55) (Swofford, 1996). Unless otherwise noted, all analyses employed the heuristic search option with tree bisection–reconnection branch swapping, MULPARS, and random addition of taxa (100 replicates). Multistate characters were interpreted as uncertainty. Phylogenetic signal within each data set was evaluated using the g_1 statistic (Fitch, 1979, 1984; Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992), which measures the skewness of the distribution of random trees (10,000 random trees were used for each analysis). Tree support was assessed using the nonparametric bootstrap (1000 replicates).

Molecular Clock

We tested whether the assumption of a molecular clock for the DNA sequence data is valid using a likelihood-ratio test (Goldman, 1993; Yang, 1996). The null hypothesis for this test is that the rate of nucleotide substitutions is constant over all branches of the tree. We first calculated the

maximum log-likelihood value ($\log L_0$) under the Hasegawa-Kishino-Yano (HKY) model (Hasegawa et al., 1985) for all possible rooting positions of the Milinkovitch sequence data unrooted tree with a molecular clock assumption enforced. The following maximum-likelihood settings were used: nucleotide frequencies estimated from the data, number of substitution types = 2, rate heterogeneity was assumed to follow a gamma distribution with the shape parameter estimated via maximum likelihood, and the transition/transversion ratio was estimated via maximum likelihood. We then calculated the maximum log-likelihood for the unrooted tree without the constraint of the molecular clock ($\log L_1$) under the same model settings. We have assumed that the deviance, $2(\log L_1 - \log L_0)$, is χ^2 distributed with $n - 2$ degrees of freedom (where n = number of taxa). The likelihood-ratio test statistic was calculated and evaluated against the χ^2 distribution using the Mathematica software package. If the maximum log-likelihood value without the molecular clock constraint is significantly larger than the log-likelihood value with the molecular clock constraint (such that $P < 0.05$), then the null hypothesis that the observed DNA sequence variation is consistent with a molecular clock is rejected. We note that it has been argued that the likelihood-ratio test statistic may not be χ^2 distributed when applied to some phylogenetic questions (Goldman, 1993; Huelsenbeck et al., 1996b). We suggest that our results will not be compromised unless the deviance is found to be close to the critical values of the χ^2 distribution (for a similar case, see Yang, 1996).

RESULTS

Phylogenetic Signal

The results of the g_1 analyses indicate that the morphological and molecular data sets contain substantial phylogenetic structure. For each independent data set as well as for combined data sets with alternative weighting procedures, the g_1 values were significantly left-skewed at $P < 0.01$ (Hillis and Huelsenbeck, 1992).

Morphological Analyses

Although we scored morphological characters for 68 cetacean taxa and the archaeocete composite terminal taxon, 17 species within the family Delphinidae (true dolphins) and the ziphiid (beaked whales) genus *Mesoplodon* had character state distributions identical with other ingroup taxa within their respective taxonomic groupings. In such cases, we retained only one representative with a given character state distribution. Therefore, our analyses of the complete data set include 51 ingroup taxa.

An analysis of the complete morphological data set (51 ingroup taxa) resulted in the recovery of more than 45,000 equally most parsimonious trees with a length of 387 steps (Fig. 1). This search was terminated before completion with more than 36,000 trees remaining to be swapped. Given that we could not complete a single full heuristic search, it was not possible to perform complete analyses on 100 random-addition replicates of the data set. In an attempt to avoid islands of equally parsimonious trees (Maddison et al., 1992), we performed limited analyses saving 25 trees for each of 100 random-addition sequence replicates and then used all of the shortest trees obtained (each with a length of 387) as starting points for further branch swapping. This search was again terminated after saving 45,000 equally most parsimonious trees. This procedure failed to find additional trees inconsistent with the strict consensus tree presented in Figure 1. The large number of equally most parsimonious trees can be attributed to the lack of resolution within Delphinidae and *Mesoplodon*. As the goal of the study is the resolution of higher level relationships among cetaceans, we gave little emphasis to a search for morphological characters that resolve relationships within these two groups. Despite the large number of equally most parsimonious trees, the well-resolved strict consensus tree is consistent with odontocete monophyly.

With the complete morphological data set, the large number of terminal taxa to-

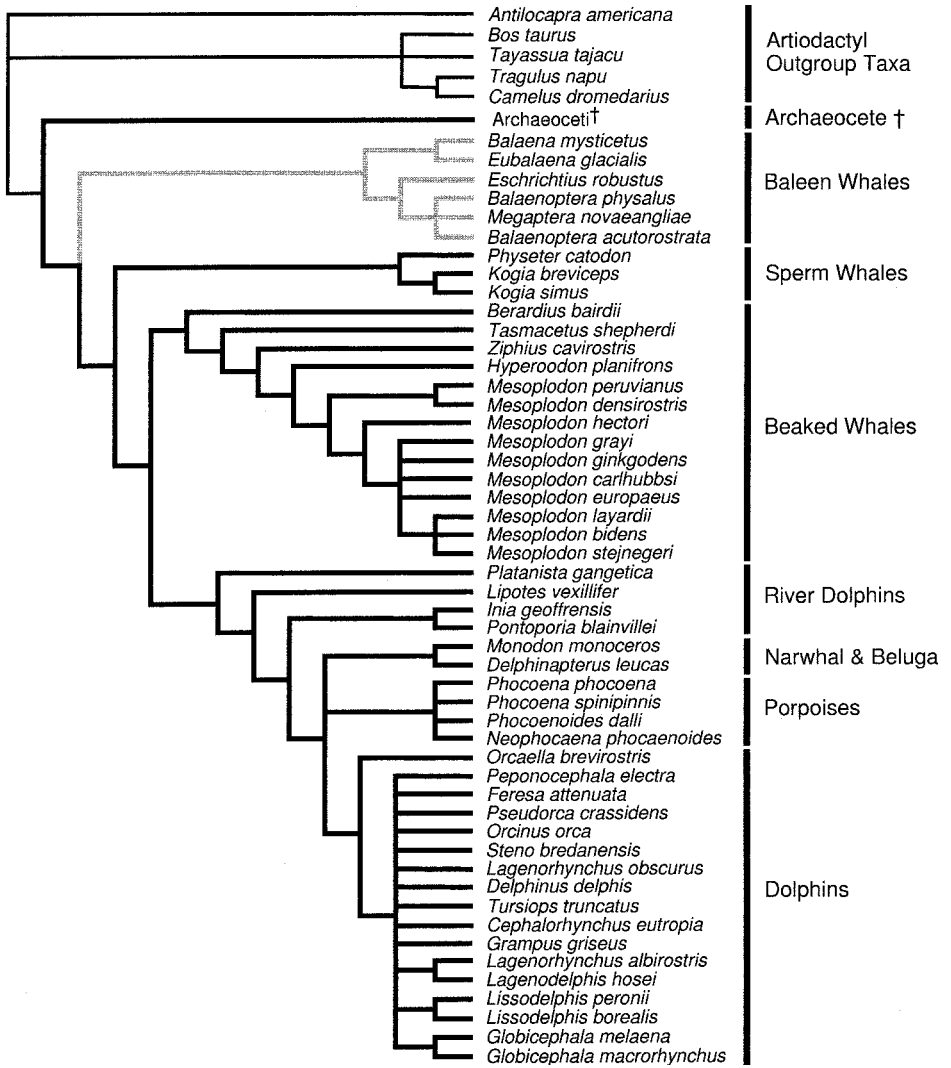

FIGURE 1. Strict consensus of 45,000 equally most parsimonious trees (length = 387) resulting from the analysis of the complete morphological data set for 51 ingroup taxa and 5 outgroup species. Seventeen taxa were excluded because they shared identical character-state distributions with other ingroup species: *Peponocephala electra* = *Sotalia fluviatilis, Sousa teuszii, Sousa chinensis, Stenella coeruleoalba, S. attenuata, S. frontalis, S. longirostris, S. clymene*; *Mesoplodon hectori* = *M. europaeus*; *Cephalorhynchus eutropia* = *C. commersoni, C. hectori, C. heavisidii*; *Phocoena phocoena* = *P. sinus*; *Lagenorhynchus obscurus* = *L. acutus, L. obliquidens, L. cruciger, L. australis.* Consistency index (CI; excluding uninformative characters) = 0.591; retention index (RI) = 0.910; rescaled consistency index (RC) = 0.555.

gether with the lack of resolution within Delphinidae and *Mesoplodon* effectively prevented us from performing a nonparametric bootstrap analysis of the complete data set. However, given our focus on higher level relationships, we pruned from our matrix several delphinid and *Mesoplodon* species that contributed to unresolved polytomies and then performed a bootstrap analysis of this reduced data set. The results of this analysis are presented in Figure 2.

Analysis of the morphological data set including only the 21 cetacean species for

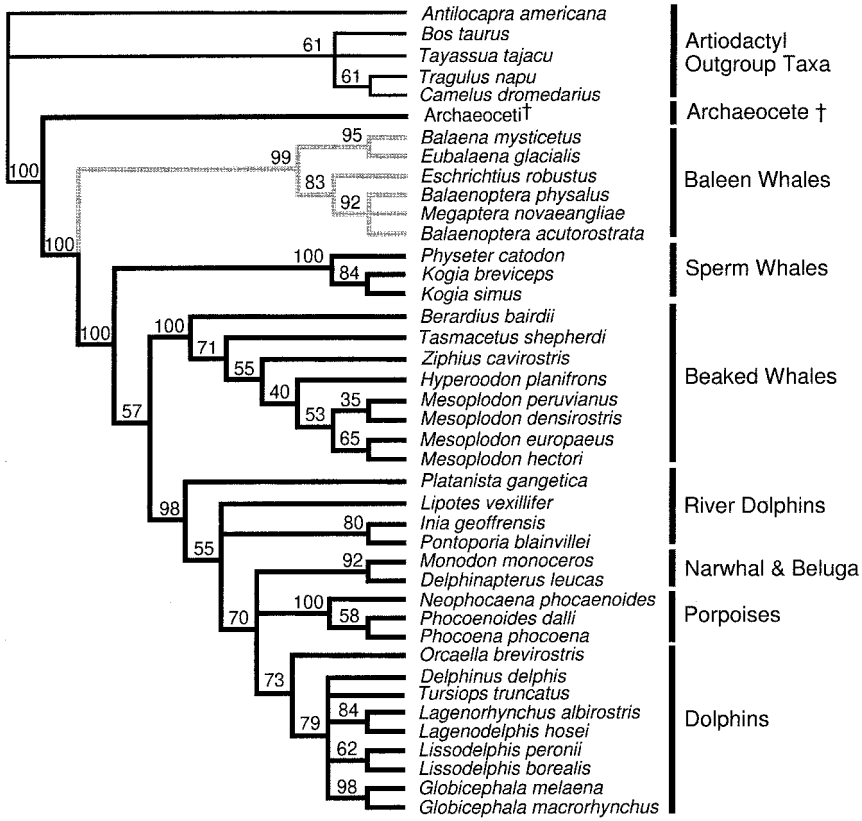

FIGURE 2. Strict consensus of 10 equally most parsimonious trees (length = 363) with nonparametric bootstrap proportions resulting from the analysis of the reduced morphological data set. To avoid computational limitations inherent in the bootstrap analysis, several delphinid and *Mesoplodon* species have been removed, leaving 41 taxa. CI (excluding uninformative characters) = 0.611; RI = 0.897; RC = 0.569.

which DNA sequence data are available plus the composite archaeocete recovered 88 equally most parsimonious trees. The strict consensus tree with bootstrap values is presented in Figure 3. This consensus tree is entirely congruent with the consensus tree resulting from the morphological analysis with 51 ingroup taxa (Fig. 1).

DNA Sequence Data Analysis

Analysis of the Milinkovitch data set produced a tree congruent with the published phylogenetic estimate of Milinkovitch et al. (1994). This estimate (Fig. 4) suggests moderate support for the monophyly of a group containing sperm and baleen whales (bootstrap value of 72% at this node) and the consequent paraphyly of Odontoceti.

The modified sequence data set included *Tragulus napu* and *Antilocapra americana* as additional outgroup species, excluded two ambiguously aligned gap regions, and incorporated a slight adjustment of the alignment to account for secondary structure. Analysis of this data set resulted in a tree rooted at *Physeter catodon* (Fig. 5). However, support for the basal nodes of this tree is weak, with several nodes receiving bootstrap values of less than 50% (Fig. 5).

Sensitivity to Outgroup Sampling

To explore the sensitivity of rooting position to choice of outgroup taxa, we analyzed the modified sequence and morphological data sets with the 31 possible combinations of the five artiodactyl outgroup species. We

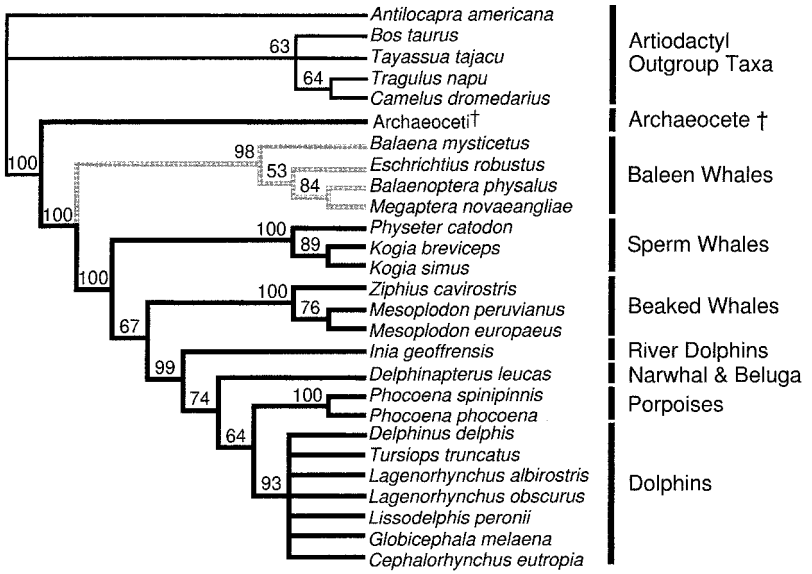

FIGURE 3. Strict consensus of 88 equally most parsimonious trees (length = 276) with nonparametric bootstrap proportions resulting from the analysis of the morphological data set. This analysis includes the 21 species of cetaceans for which sequence data are available, the archaeocete composite taxon, and the 5 artiodactyl species comprising the outgroup. CI (excluding uninformative characters) = 0.722; RI = 0.916; RC = 0.687.

also analyzed the Milinkovitch data set with the seven possible combinations of their three outgroup species. We found the results of the morphological analyses to be insensitive to choice of outgroup taxa. With all 31 combinations, the same rooting position was obtained. However, the results based on the molecular data sets varied depending upon which outgroup taxa were included in the analysis. In the 31 analyses employing different outgroup combinations for the modified sequence data, we recovered seven alternative rooting positions on two unrooted trees (Fig. 6a). Note that some outgroup combinations recovered several equally most parsimonious trees, often including multiple alternative rooting points and occasionally including both unrooted trees. In analyses with 30 of the 31 outgroup combinations, an unrooted tree that is inconsistent with either the traditional or the Milinkovitch et al. (1993, 1994) hypotheses of cetacean relationships (i.e., it is impossible to root this unrooted tree in a manner consistent with either the traditional or Milinkovitch phylogenetic hypotheses) is the most parsimonious reconstruction or at least is equally parsimonious with the alternative unrooted tree. The second unrooted tree, which is consistent with the traditional and Milinkovitch hypotheses, is at least equally parsimonious with the alternative unrooted tree under 6 of the 31 possible outgroup combinations. The two most common rooting positions (A and B) place either *Physeter* (20 of 31 outgroup combinations) or Ziphiidae (13 of 31 outgroup combinations) as the sister group to the remaining cetaceans. A clade composed of Physeteridae + baleen whales (the primary Milinkovitch hypothesis) is recovered with three outgroup combinations (rooting positions E and G). The traditional hypothesis of odontocete monophyly is an equally most parsimonious solution with 1 of 31 outgroup combinations (rooting position F).

Analysis of the Milinkovitch sequence data with the seven possible outgroup combinations discovered four alternative rooting positions on two unrooted trees (Fig. 6b). One of the two unrooted trees is identical with one of the unrooted trees recovered in the 31 combination analysis, whereas the other is a novel reconstruction

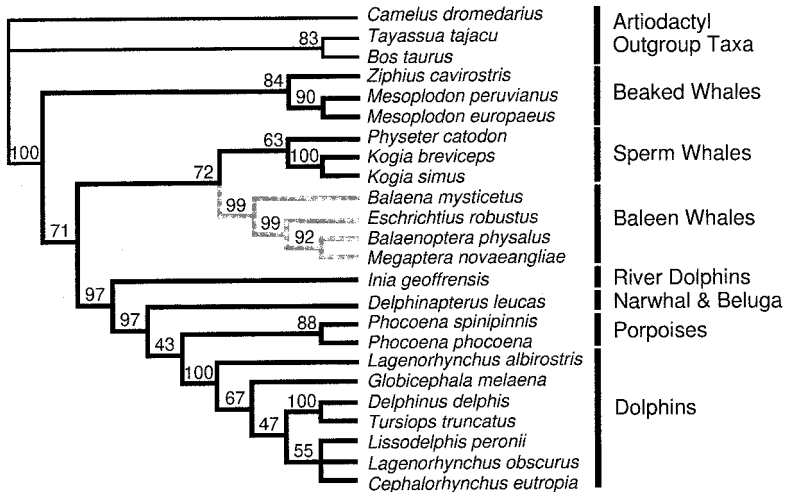

FIGURE 4. Strict consensus of two equally most parsimonious trees (length = 2,074) resulting from the analysis of the Milinkovitch DNA sequence data. Nonparametric bootstrap proportions are provided at each node. Consistency indices are not provided because the DNA sequence characters were weighted using step matrices.

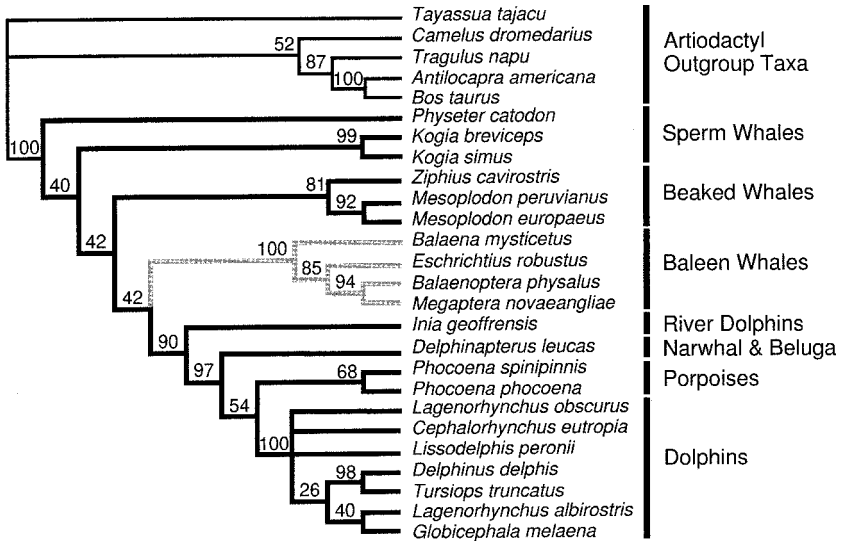

FIGURE 5. Strict consensus of three equally most parsimonious trees (length = 1,664) resulting from the analysis of the modified DNA sequence data. The modified treatment of the sequence data differed from the Milinkovitch treatment only in the exclusion of two ambiguously aligned regions of the 12S and 16S sequences together with their corresponding gap characters, our inclusion of two additional species of artiodactyl outgroup taxa (*Antilocapra americana, Tragulus napu*), and our adjustment of the alignment of one small gap in the 16S sequence to reconcile its positional homology with constraints imposed by secondary structure of the ribosomal RNA. Nonparametric bootstrap proportions are provided at each node. Consistency indices are not provided because the DNA sequence characters were weighted using step matrices.

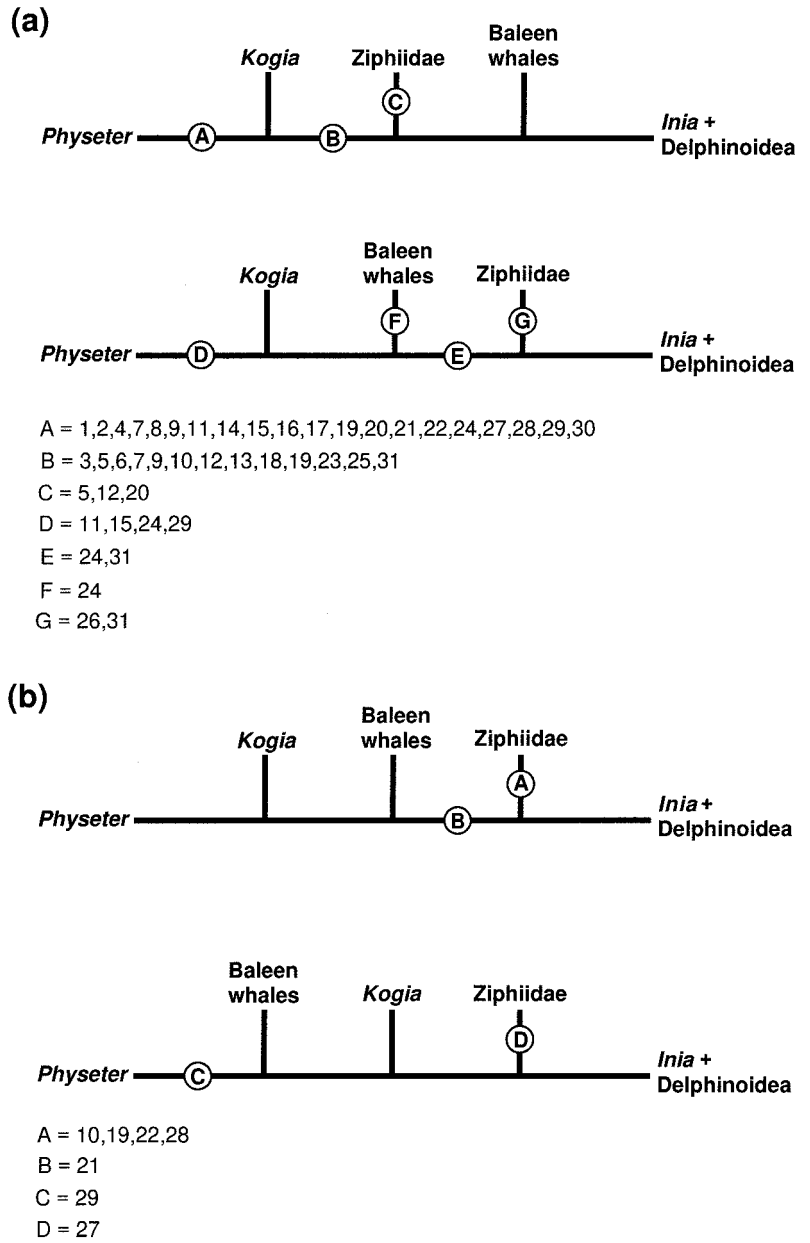

FIGURE 6. Unrooted DNA sequence trees with alternative rooting points (enclosed letters) obtained with (a) the 31 possible combinations of the outgroup taxa with the modified sequence data and (b) the seven possible outgroup combinations with the Milinkovitch data. The numbers following the rooting-position labels refer to alternative combinations of outgroup taxa. The outgroup taxa corresponding to each number are as follows: 1. *T. tajacu, C. dromedarius, T. napu, B. taurus, A. americana*; 2. *T. tajacu, C. dromedarius, T. napu, B. taurus*; 3. *T. tajacu, C. dromedarius, T. napu, A. americana*; 4. *T. tajacu, T. napu, B. taurus, A. americana*; 5. *C. dromedarius, T. napu, B. taurus, A. americana*; 6. *T. tajacu, C. dromedarius, B. taurus, A. americana*; 7. *T. tajacu, C. dromedarius, T. napu*; 8. *T. tajacu, T. napu, B. taurus*; 9. *C. dromedarius, T. napu, B. taurus*; 10. *T. tajacu, C. dromedarius, B. taurus*; 11. *T. tajacu, T. napu, A. americana*; 12. *C. dromedarius, T. napu, A. americana*; 13. *T. tajacu, C. dromedarius, A. americana*; 14. *T. napu, B. taurus, A. americana*; 15. *T. tajacu, B. taurus, A. americana*; 16. *C. dromedarius, B. taurus, A. americana*; 17. *T. tajacu, T. napu*; 18. *C. dromedarius, T. napu*; 19. *T. tajacu, C. dromedarius*; 20. *T. napu, B. taurus*; 21. *T. tajacu, B. taurus*; 22. *C. dromedarius, B. taurus*; 23. *T. napu, A. americana*; 24. *T. tajacu, A. americana*; 25. *B. taurus, A. americana*; 26. *C. dromedarius, A. americana*; 27. *B. taurus*; 28. *C. dromedarius*; 29. *T. tajacu*; 30. *T. napu*; 31. *A. americana*.

that requires Physeteridae to be paraphyletic. Results obtained with five of the seven outgroup combinations are consistent with the Milinkovitch et al. (1993, 1994) hypothesis of a Physeteridae + Mysticeti clade (rooting positions A and B), whereas none of the combinations results in a phylogenetic estimate consistent with toothed-whale monophyly.

Sensitivity to Alternative Treatments of Ambiguously Aligned Gap Regions

Realignment of the gap regions employing gap penalties of one through five produced alignments distinct from that of Milinkovitch et al. (1993, 1994), although gap penalties of four and five produced identical alignments. Analysis of the molecular data following the Milinkovitch protocols, but incorporating the realigned gap regions, resulted in three phylogenetic estimates, none of which agrees with the Milinkovitch et al. (1994) published tree (Fig. 7). In each case, these trees differ from the Milinkovitch et al. (1994) tree in placing baleen whales as the sister group of *Inia* + Delphinoidea rather than Physeteridae (consistent with the findings of Arnason and Gullberg, 1994). Alignments based on gap penalties of one, two, four, and five result in trees rooted at Ziphiidae (as suggested by Milinkovitch et al., 1993, 1994), whereas the alignment based on a gap penalty of three results in a tree rooted at *Physeter*. When we removed the two gap regions from consideration, the Physeteridae + Mysticeti clade again was lost, resulting in a trichotomy of Mysticeti, Physeteridae, and *Inia* + Delphinoidea.

Templeton Test

Although it is clear that the molecular rooting positions are sensitive to choice of outgroup taxa, it is unclear whether the molecular and morphological rooting positions differ significantly from one another. We attempted to address this question by performing the Templeton test (Templeton, 1983; Larson, 1994) for each data set. This nonparametric test determines whether a data set is significantly incompatible with an alternative tree under the null hypothesis that the data sets are equally likely to support the two trees. We used this test to determine whether the molecular data are significantly incompatible with odontocete monophyly, as well as whether the morphological data are incompatible with the alternative molecular rooting positions or the proposed Mysticeti + Physeteridae clade. We performed two-tailed Wilcoxon signed rank tests (following the recommendation of Felsenstein, 1985) using the StatView 4.01 statistical package. This program can account for ties in the calculation of P values, and all of our reported P values are tie adjusted. We employed the same sets of assumptions in our application of the Templeton test that we used in the parsimony analyses, including the use of differential character weighting of transitions and transversions.

When we analyzed the Milinkovitch sequence data under the constraint of odontocete monophyly, the increase in number of steps was significant ($P = 0.008$, $T_s = 57.0$, $n = 24$). When we analyzed the modified sequence data under the same constraint, we obtained a nonsignificant result ($P = 0.48$, $T_s = 104.5$, $n = 22$). These results indicate that the sequence data conflict less with odontocete monophyly under the assumptions of the modified treatment than they do under the Milinkovitch assumptions.

With the morphological data set, we performed three separate analyses in which we constrained the tree topology to match results of the molecular phylogenetic analyses. One analysis included a constraint tree forcing beaked whales to be the sister group of the remaining cetaceans (the weakly supported rooting position reported by Milinkovitch et al., 1993, 1994). In a second analysis, we forced *Physeter catodon* to be the sister taxon of the remaining species of cetaceans (as suggested by the realigned molecular data when all five artiodactyl outgroup taxa are included). The third analysis constrained sperm whale + baleen whale monophyly (regardless of rooting position), as suggested by our analyses of the Milinkovitch molecular data and the primary conclusion of the

Milinkovitch et al. (1993, 1994) papers. All three analyses found that the morphological data very strongly reject the alternative molecular branching arrangements ($P < 0.0003$, $T_s = 64.0$, $n = 31$ for the Ziphiidae rooting position; $P < 0.0001$, $T_s = 15.5$, $n = 30$ for the *Physeter* rooting position; $P < 0.0005$, $T_s = 24.0$, $n = 23$ for sperm whale + baleen whale monophyly).

Partition-Homogeneity Tests

Before proceeding to combined-data analyses, we performed partition-homogeneity tests (Farris et al., 1995) to assess whether the morphological and molecular data sets are significantly incongruent. The results of these analyses differed depending on our treatment of the molecular data. When the morphological data are analyzed together with the modified sequence data, the null hypothesis of data-set homogeneity cannot be rejected ($P = 0.51$ with morphological characters weighted as transitions, $P = 0.29$ with morphological characters weighted as transversions). When the morphological and Milinkovitch sequence data are analyzed, the null hypothesis of data set homogeneity is rejected ($P = 0.01$), whether morphological characters are weighted equivalently with transitions or transversions.

Combined-Data Analyses

We based combined data analyses on the same four data treatments for which the partition-homogeneity tests were performed (Milinkovitch and modified sequence data with morphological characters weighted equivalently with either transitions or transversions). Analysis of the four data sets resulted in highly congruent strict consensus trees differing only in the resolution of relationships within Delphinidae and in the outgroup topology (Figs. 8, 9). The consensus trees are congruent with the consensus tree obtained in the analysis of the morphology-only data set and suggest strong support for the monophyly of several cetacean lineages including Odontoceti. Because the issue of odontocete monophyly is particularly contentious, we provide a list of unambiguous odontocete synapomorphies obtained in the combined analyses of the morphological and modified sequence data to allow the character support for this node to be evaluated (Table 1).

Nonparametric bootstrap analyses of the combined data sets (Figs. 8, 9) result in strict consensus trees that are congruent with the morphology-only bootstrap consensus tree (Fig. 3). Furthermore, the results indicate that bootstrap support increases at most nodes when compared with the morphology-only bootstrap results. In the analyses combining the morphological and modified sequence data, the weight assigned to morphological characters has relatively little effect on the observed bootstrap values. When morphological characters are weighted equivalently with transversions, bootstrap support increases relative to the morphology-only bootstrap analysis at every node not already supported by bootstrap values of 100%. Under these assumptions, monophyly of extant cetaceans, Mysticeti, Odontoceti, Physeteridae, *Kogia,* Ziphiidae, *Inia geoffrensis* + Delphinoidea, Phocoenidae, and Delphinidae are each supported with bootstrap values of 100% and Delphinoidea receives a bootstrap value of 99% (Fig. 8). When morphological characters are weighted equivalently with transitions, extant cetaceans, Mysticeti, *Kogia,* Ziphiidae, *Inia* + Delphinoidea, and Delphinidae retain bootstrap values of 100%; Odontoceti and Phocoenidae have bootstrap values of 99%; and Physeteridae and Delphinoidea have bootstrap support of 98% (Fig. 8).

The weight assigned to morphological characters in analyses combining the morphological and Milinkovitch sequence data affects the relative support for odontocete monophyly (Fig. 9). The morphology + Milinkovitch analyses with morphological characters weighted as transversions essentially duplicate the results obtained in the analyses combining the morphological data with the modified sequence data, with bootstrap support increasing over the morphology-only analysis at every node not already receiving bootstrap support of 100% except one (Phocoenidae + Delphinidae). When morphological characters are

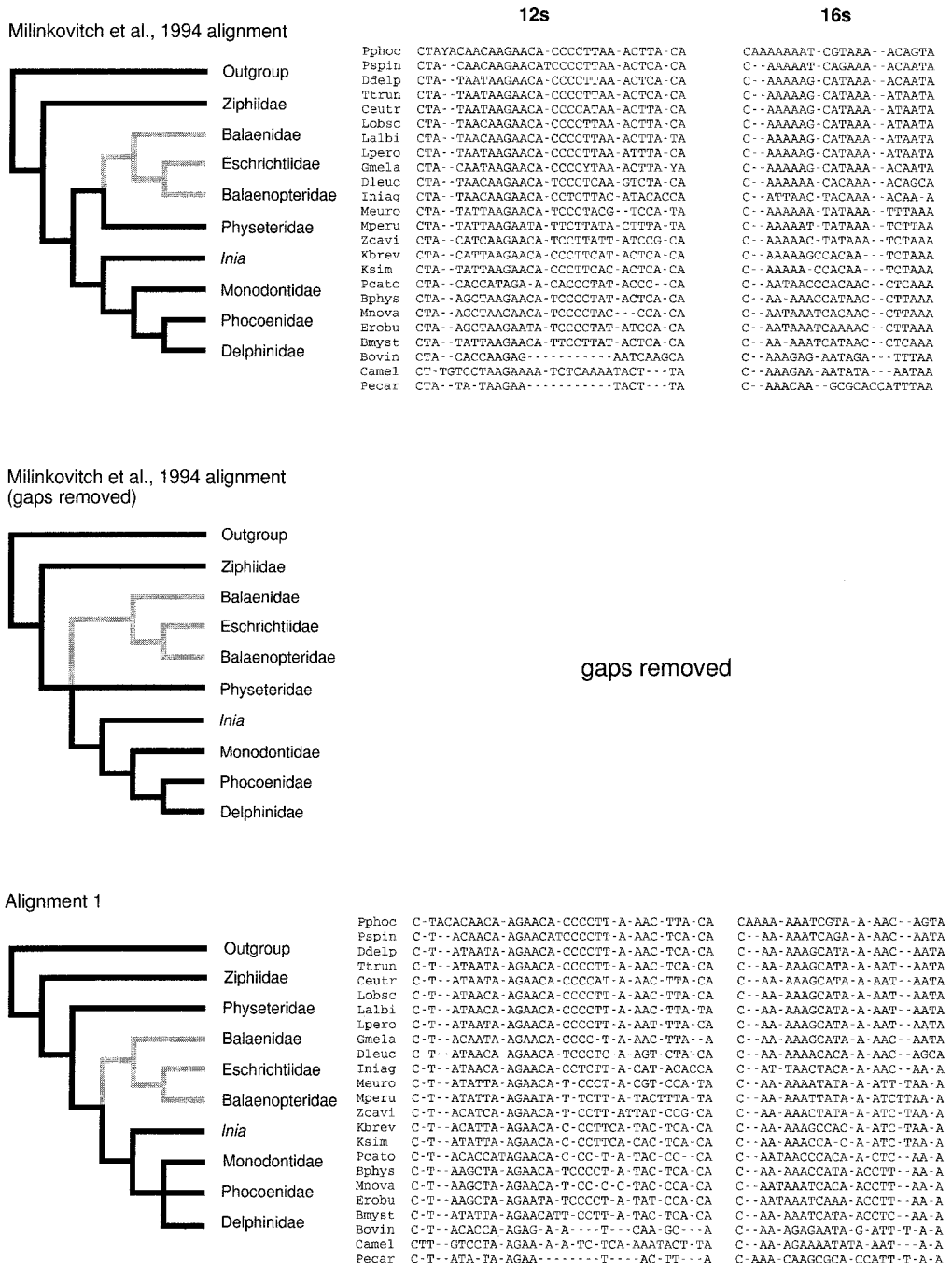

FIGURE 7. Results of the analysis exploring the effects of gap treatment with the Milinkovitch et al. (1994) data set. The resulting strict consensus trees are placed adjacent to the ambiguously aligned 12S and 16S sequences. The first block provides the actual alignment employed by Milinkovitch et al. (1994) and the resulting strict consensus tree. The second block provides the results when the ambiguously aligned gap regions are removed from consideration in the analysis. The remaining blocks present the results when the ambiguously aligned regions were realigned with gap penalties of one through five.

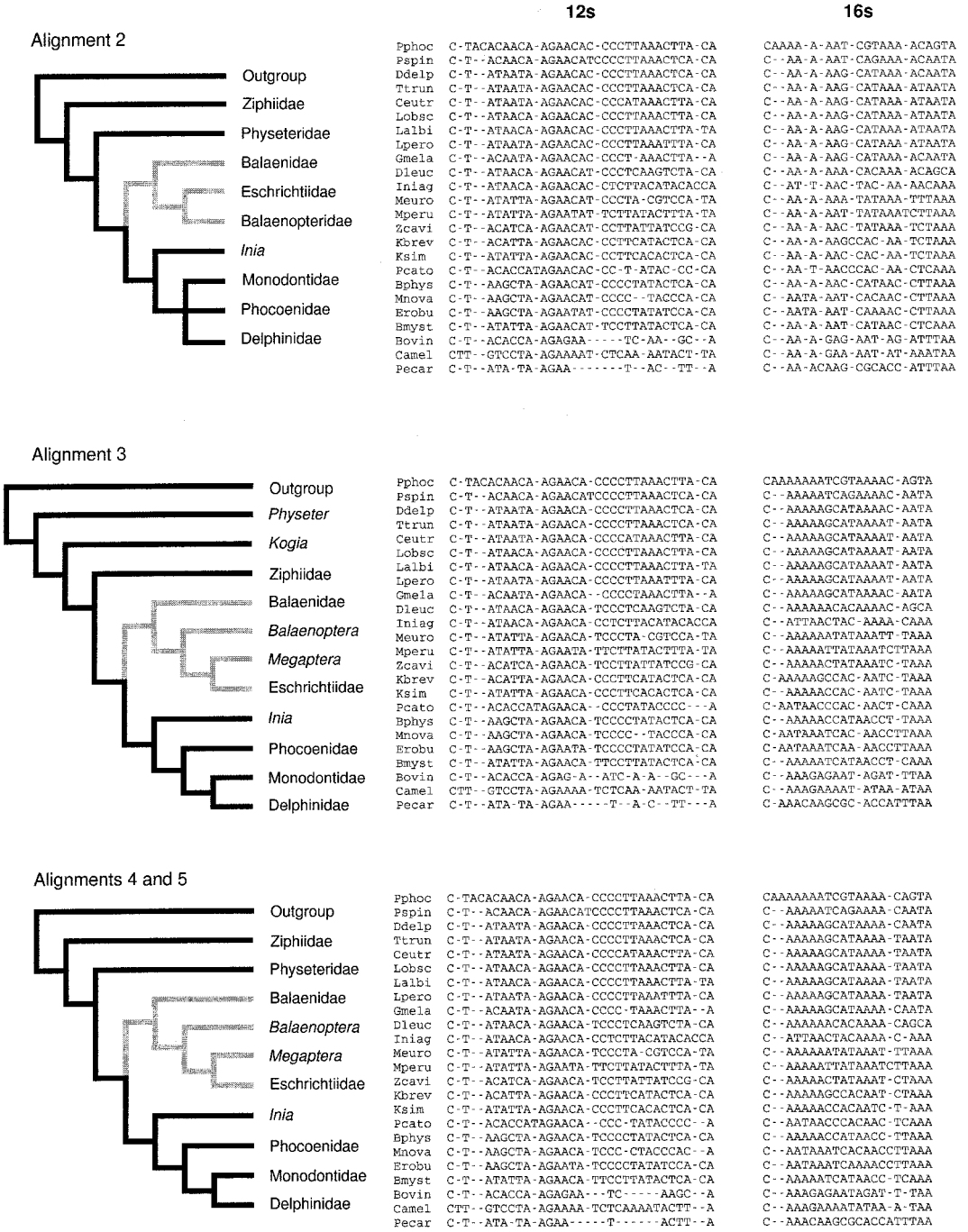
12s
16s
Alignment 2
Outgroup
Ziphiidae
Physeteridae
Balaenidae
Eschrichtiidae
Balaenopteridae
Inia
Monodontidae
Phocoenidae
Delphinidae
Pphoc C-TACACAACA-AGAACAC-CCCTTAAACTTA-CA CAAAA-A-AAT-CGTAAA-ACAGTA
Pspin C-T--ACAACA-AGAACATCCCCTTAAACTCA-CA C--AA-A-AAT-CAGAAA-ACAATA
Ddelp C-T--ATAATA-AGAACAC-CCCTTAAACTCA-CA C--AA-A-AAG-CATAAA-ACAATA
Ttrun C-T--ATAATA-AGAACAC-CCCTTAAACTCA-CA C--AA-A-AAG-CATAAA-ATAATA
Ceutr C-T--ATAATA-AGAACAC-CCCATAAACTTA-CA C--AA-A-AAG-CATAAA-ATAATA
Lobsc C-T--ATAACA-AGAACAC-CCCTTAAACTTA-CA C--AA-A-AAG-CATAAA-ATAATA
Lalbi C-T--ATAACA-AGAACAC-CCCTTAAACTTA-TA C--AA-A-AAG-CATAAA-ATAATA
Lpero C-T--ATAATA-AGAACAC-CCCTTAAATTTA-CA C--AA-A-AAG-CATAAA-ATAATA
Gmela C-T--ACAATA-AGAACAC-CCCT-AAACTTA--A C--AA-A-AAG-CATAAA-ACAATA
Dleuc C-T--ATAACA-AGAACAT-CCCTCAAGTCTA-CA C--AA-A-AAA-CACAAA-ACAGCA
Iniag C-T--ATAACA-AGAACAC-CTCTTACATACACCA C--AT-T-AAC-TAC-AA-AACAAA
Meuro C-T--ATATTA-AGAACAT-CCCTA-CGTCCA-TA C--AA-A-AAA-TATAAA-TTTTAAA
Mperu C-T--ATATTA-AGAATAT-TCTTATACTTTA-TA C--AA-A-AAT-TATAAATCTTAAA
Zcavi C-T--ACATCA-AGAACAT-CCTTATTATCCG-CA C--AA-A-AAC-TATAAA-TCTAAA
Kbrev C-T--ACATTA-AGAACAC-CCTTCATACTCA-CA C--AA-A-AAGCCAC-AA-TCTAAA
Ksim C-T--ATATTA-AGAACAC-CCTTCACACTCA-CA C--AA-A-AAC-CAC-AA-TCTAAA
Pcato C-T--ACACCATAGAACAC-CC-T-ATAC-CC-CA C--AA-T-AACCCAC-AA-CTCAAA
Bphys C-T--AAGCTA-AGAACAT-CCCCTATACTCA-CA C--AA-A-AAC-CATAAC-CTTAAA
Mnova C-T--AAGCTA-AGAACAT-CCCC--TACCCA-CA C--AATA-AAT-CACAAC-CTTAAA
Erobu C-T--AAGCTA-AGAATAT-CCCCTATATCCA-CA C--AATA-AAT-CAAAAC-CTTAAA
Bmyst C-T--ATATTA-AGAACAT-TCCTTATACTCA-CA C--AA-A-AAT-CATAAC-CTCAAA
Bovin C-T--ACACCA-AGAGAA-----TC-AA--GC--A C--AA-A-GAG-AAT-AG-ATTTAA
Camel CTT--GTCCTA-AGAAAAT-CTCAA-AATACT-TA C--AA-A-GAA-AAT-AT-AAATAA
Pecar C-T--ATA-TA-AGAA-------T--AC--TT--A C--AA-ACAAG-CGCACC-ATTTAA
Alignment 3
Outgroup
Physeter
Kogia
Ziphiidae
Balaenidae
Balaenoptera
Megaptera
Eschrichtiidae
Inia
Phocoenidae
Monodontidae
Delphinidae
Pphoc C-TACACAACA-AGAACA-CCCCTTAAACTTA-CA CAAAAAAATCGTAAAAC-AGTA
Pspin C-T--ACAACA-AGAACATCCCCTTAAACTCA-CA C--AAAAATCAGAAAAC-AATA
Ddelp C-T--ATAATA-AGAACA-CCCCTTAAACTCA-CA C--AAAAAGCATAAAAC-AATA
Ttrun C-T--ATAATA-AGAACA-CCCCTTAAACTCA-CA C--AAAAAGCATAAAAT-AATA
Ceutr C-T--ATAATA-AGAACA-CCCCATAAACTTA-CA C--AAAAAGCATAAAAT-AATA
Lobsc C-T--ATAACA-AGAACA-CCCCTTAAACTTA-CA C--AAAAAGCATAAAAT-AATA
Lalbi C-T--ATAACA-AGAACA-CCCCTTAAACTTA-TA C--AAAAAGCATAAAAT-AATA
Lpero C-T--ATAATA-AGAACA-CCCCTTAAATTTA-CA C--AAAAAGCATAAAAT-AATA
Gmela C-T--ACAATA-AGAACA--CCCCTAAACTTA--A C--AAAAAGCATAAAAC-AATA
Dleuc C-T--ATAACA-AGAACA-TCCCTCAAGTCTA-CA C--AAAAAACACAAAA-AGCA
Iniag C-T--ATAACA-AGAACA-CCTCTTACATACACCA C--ATTAACTAC-AAAA-CAAA
Meuro C-T--ATATTA-AGAACA-TCCCTA-CGTCCA-TA C--AAAAAATATAAATT-TAAA
Mperu C-T--ATATTA-AGAATA-TTCTTATACTTTA-TA C--AAAAATTATAAATCTTAAA
Zcavi C-T--ACATCA-AGAACA-TCCTTATTATCCG-CA C--AAAAACTATAAATC-TAAA
Kbrev C-T--ACATTA-AGAACA-CCCTTCATACTCA-CA C-AAAAAGCCAC-AATC-TAAA
Ksim C-T--ATATTA-AGAACA-CCCTTCACACTCA-CA C--AAAAACCAC-AATC-TAAA
Pcato C-T--ACACCATAGAACA--CCCTATACCCC---A C-AATAACCCAC-AACT-CAAA
Bphys C-T--AAGCTA-AGAACA-TCCCCTATACTCA-CA C--AAAAACCATAACCT-TAAA
Mnova C-T--AAGCTA-AGAACA-TCCCC--TACCCA-CA C-AATAAATCAC-AACCTTAAA
Erobu C-T--AAGCTA-AGAATA-TCCCCTATATCCA-CA C-AATAAATCAA-AACCTTAAA
Bmyst C-T--ATATTA-AGAACA-TTCCTTATACTCA-CA C--AAAAATCATAACCT-CAAA
Bovin C-T--ACACCA-AGAG-A--ATC-A-A--GC---A C--AAAGAGAAT-AGAT-TTAA
Camel CTT--GTCCTA-AGAAAA-TCTCAA-AATACT-TA C--AAAGAAAAT-ATAA-ATAA
Pecar C-T--ATA-TA-AGAA-----T--A-C--TT---A C-AAACAAGCGC-ACCATTTAA
Alignments 4 and 5
Outgroup
Ziphiidae
Physeteridae
Balaenidae
Balaenoptera
Megaptera
Eschrichtiidae
Inia
Phocoenidae
Monodontidae
Delphinidae
Pphoc C-TACACAACA-AGAACA-CCCCTTAAACTTA-CA CAAAAAAATCGTAAAA-CAGTA
Pspin C-T--ACAACA-AGAACATCCCCTTAAACTCA-CA C--AAAAATCAGAAAA-CAATA
Ddelp C-T--ATAATA-AGAACA-CCCCTTAAACTCA-CA C--AAAAAGCATAAAA-CAATA
Ttrun C-T--ATAATA-AGAACA-CCCCTTAAACTCA-CA C--AAAAAGCATAAAA-TAATA
Ceutr C-T--ATAATA-AGAACA-CCCCATAAACTTA-CA C--AAAAAGCATAAAA-TAATA
Lobsc C-T--ATAACA-AGAACA-CCCCTTAAACTTA-CA C--AAAAAGCATAAAA-TAATA
Lalbi C-T--ATAACA-AGAACA-CCCCTTAAACTTA-TA C--AAAAAGCATAAAA-TAATA
Lpero C-T--ATAATA-AGAACA-CCCCTTAAATTTA-CA C--AAAAAGCATAAAA-TAATA
Gmela C-T--ACAATA-AGAACA-CCCC-TAAACTTA--A C--AAAAAGCATAAAA-CAATA
Dleuc C-T--ATAACA-AGAACA-TCCCTCAAGTCTA-CA C--AAAAAACACAAAA-CAGCA
Iniag C-T--ATAACA-AGAACA-CCTCTTACATACACCA C--ATTAACTACAAAA-C-AAA
Meuro C-T--ATATTA-AGAACA-TCCCTA-CGTCCA-TA C--AAAAAATATAAAT-TTAAA
Mperu C-T--ATATTA-AGAATA-TTCTTATACTTTA-TA C--AAAAATTATAAATCTTAAA
Zcavi C-T--ACATCA-AGAACA-TCCTTATTATCCG-CA C--AAAAACTATAAAT-CTAAA
Kbrev C-T--ACATTA-AGAACA-CCCTTCATACTCA-CA C--AAAAAGCCACAAT-CTAAA
Ksim C-T--ATATTA-AGAACA-CCCTTCACACTCA-CA C--AAAAACCACAATC-T-AAA
Pcato C-T--ACACCATAGAACA--CCC-TATACCCC--A C--AATAACCCACAAC-TCAAA
Bphys C-T--AAGCTA-AGAACA-TCCCCTATACTCA-CA C--AAAAACCATAACC-TTAAA
Mnova C-T--AAGCTA-AGAACA-TCCC-CTACCCAC--A C--AATAAATCACAACCTTAAA
Erobu C-T--AAGCTA-AGAATA-TCCCCTATATCCA-CA C--AATAAATCAAAACCTTAAA
Bmyst C-T--ATATTA-AGAACA-TTCCTTATACTCA-CA C--AAAAATCATAACC-TCAAA
Bovin C-T--ACACCA-AGAGAA---TC-----AAGC--A C--AAAGAGAATAGAT-T-TAA
Camel CTT--GTCCTA-AGAAAA-TCTCAAAATACTT--A C--AAAGAAAATATAA-A-TAA
Pecar C-T--ATA-TA-AGAA-----T------ACTT--A C--AAACAAGCGCACCATTTAA

FIGURE 7. Continued.

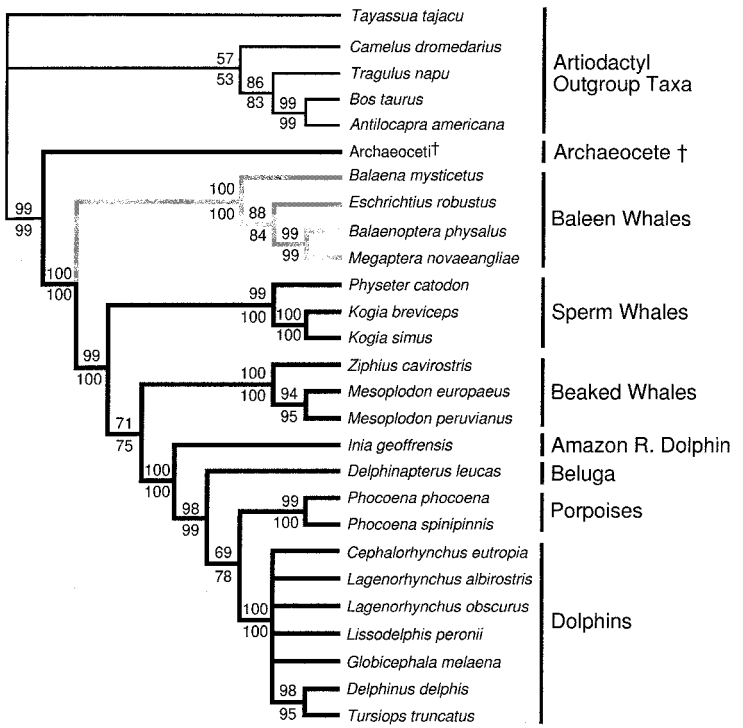

FIGURE 8. Strict consensus of trees obtained in the combined analysis of the morphology + modified DNA sequence data set with morphological characters weighted equivalently with either transitions or transversions. With morphological characters weighted as transitions, tree length = 1,950, CI (excluding uninformative characters) = 0.675, RI = 0.889, and RC = 0.649. With morphological characters weighted as transversions, tree length = 2,508, CI (excluding uninformative characters) = 0.699, RI = 0.904, and RC = 0.666. The consistency indices apply only to the morphological characters because the DNA sequence characters were weighted using step matrices. The numbers above and below each node are the bootstrap values with morphological characters weighted as transitions and transversions, respectively.

weighted equivalently with transitions, bootstrap support again increases at nearly every node, but relative bootstrap support for odontocete monophyly falls to 85%.

We performed a combined-data analysis of 51 ingroup taxa and 5 outgroup artiodactyl species. In this analysis, we combined the morphological and modified sequence data sets, and weighted morphological characters equivalent with transversions. Because of the large amount of missing data (sequence data are unavailable for 30 of 56 taxa) and because the morphological data provide little resolution within Delphinidae and *Mesoplodon,* this analysis was plagued by more severe computational limitations than the analysis of the complete morphological data set. In this case, 100 random-addition replicates were analyzed, saving a maximum of 10 trees per replicate. The minimum-length trees were used as a starting point for further branch swapping, and the analysis was terminated after saving 45,000 equally most parsimonious trees. The strict consensus tree obtained in this analysis was identical with that obtained in the analysis of the morphological data set for the same set of 51 taxa (Fig. 1), except that in the combined-data analysis, *Lagenorhynchus obscurus* and *Cephalorhynchus eutropia* were placed as sister taxa.

Finally, although the present study is focused on our morphological data set and the 12S, 16S, and cytochrome *b* sequence data of Milinkovitch et al. (1994), additional data are available for a subset of our ingroup taxa including a restriction-site data set (Ohland et al., 1995) and a myoglobin

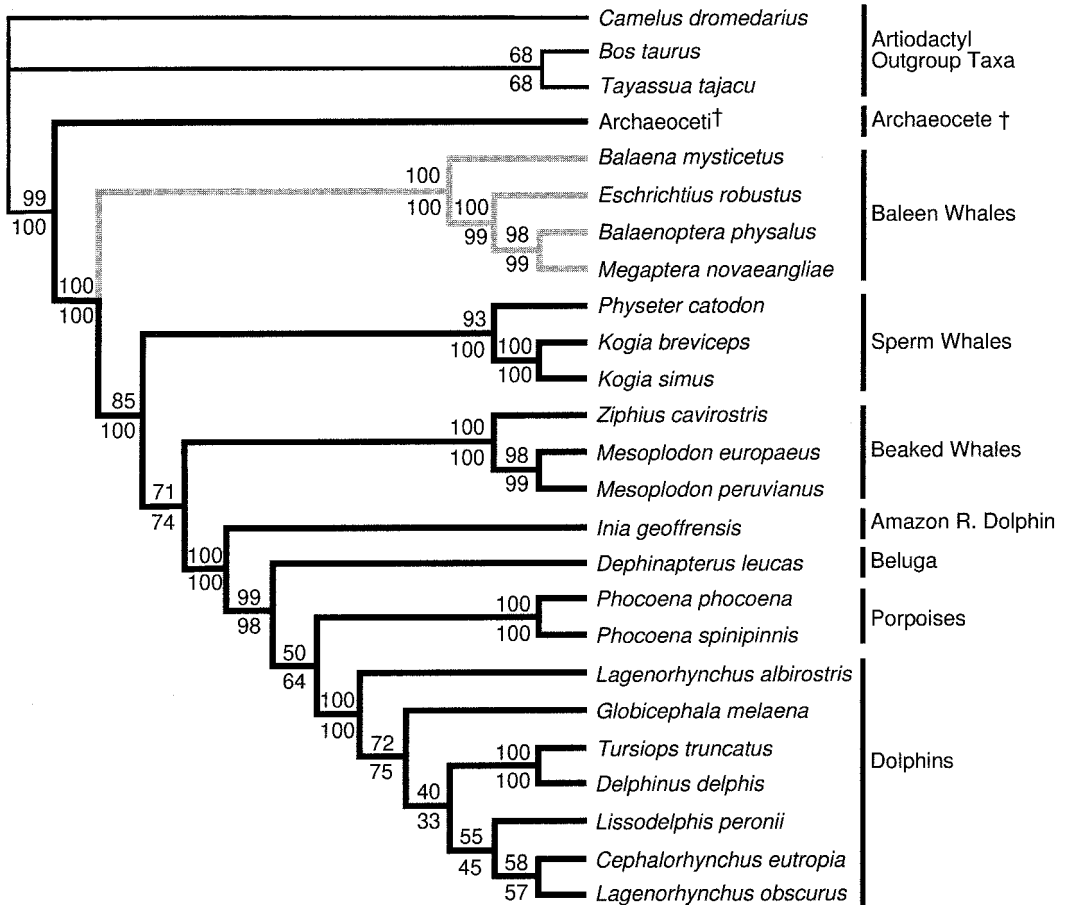

FIGURE 9. Strict consensus of trees obtained in the combined analysis of the morphology + Milinkovitch DNA sequence data set with morphological characters weighted equivalently with either transitions or transversions. With morphological characters weighted as transitions, tree length = 2,390, CI (excluding uninformative characters) = 0.720, RI = 0.894, and RC = 0.671. With morphological characters weighted as transversions, tree length = 2,980, CI (excluding uninformative characters) = 0.729, RI = 0.898, and RC = 0.681. The consistency indices apply only to the morphological characters because the DNA sequence characters were weighted using step matrices. The numbers above and below each node are the bootstrap values with morphological characters weighted as transitions and transversions, respectively.

amino acid sequence data set (analyzed by Milinkovitch et al., 1993, but not considered by Milinkovitch et al., 1994). To assess whether inclusion of these data would affect our results, we reanalyzed the restriction site and myoglobin data separately and in a 27-taxa combined-data analysis with the morphological and modified DNA sequence data. Analysis of the restriction site data set resulted in an unrooted tree that is consistent with the morphological and molecular unrooted trees (see Ohland et al., 1995). However, restriction-site data are unavailable for outgroup species, and these data could not influence the rooting position of the combined-data tree. Analysis of the myoglobin sequence data recovered a strict consensus tree unresolved at the basal nodes such that neither a baleen + sperm whale clade nor an odontocete clade was represented. Thus neither the restriction-site nor the myoglobin data sets are particularly informative with respect to the issue of odontocete

TABLE 1. The following character list includes all of the synapomorphies discovered in the combined analysis of the morphological and modified sequence data that support the monophyly of Odontoceti. We also list potential synapomorphies that include (1) ambiguously placed transformations that support the odontocete node under either ACCTRAN or DELTRAN optimization but not both and (2) characters in which odontocetes share one state and baleen whales share another but the outgroup taxa are coded with question marks. The character state in bold indicates the derived state for odontocetes. The complete morphological character list is presented in Appendix 2.

Unambiguous synapomorphies

1181. Cytochrome *b*: A $\rightarrow$**C**.
1398. Facial plane (sagittal): **(0) concave**, (1) flat to convex.
1399. Cranial vertex: (0) symmetric, **(1) asymmetric**.
1402. Premaxillae: (0) symmetric, **(1) asymmetric**.
1413. Premaxillary foramen: (0) absent, **(1) present**.
1419. Maxillae: (0) abut supraorbital processes of frontal, **(1) overlay supraorbital process**.
1423. Maxillae: (0) no maxillonasolabialis m. insertion, **(1) maxillonasolabialis m. insertion**.
1426. Antorbital notch: (0) absent, **(1) present**.
1432. Nasals (dorsal view): **(0) anteroposteriorly compressed**, (1) anteroposteriorly elongate.
1445. Pterygoids: **(0) meet at midline**, (1) separated.
1446. Lateral plate of pterygoids: (0) present, **(1) absent**.
1450. Pterygoid hamuli: **(0) meet at midline**, (1) separated.
1455. Mesethmoid: (0) roofed over by nasals, **(1) exposed dorsally**.
1456. Ethmoturbinal bones: (0) present, **(1) absent**.
1490. Anterior process of periotic/cranium attachment: (0) bony, **(1) ligamentous**.
1491. Posterior process of periotic/squamosal-occipital attachment: (0) bony, **(1) ligamentous**.
1493. Size of bone of posterior process of the periotic: (0) large, **(1) small**.
1508. Panbone in mandible: (0) absent, **(1) present**.
1531. Proximal sacs of the nasal passages: (0) absent, **(1) present**.
1573. Nucleus of lateral olfactory nerve tract: (0) present, **(1) absent**.
1578. Tympanic membrane: (0) present, **(1) reduced to "glove finger."**
1579. Tympanic bulla/ramus attachment: (0) absent, **(1) attached with band of fibrous tissue**.
1580. Middle ear ossicle/bulla attachment: (0) ligamentous, **(1) fused (joints stiffened)**.

Ambiguously placed potential synapomorphies

258. 12S ribosomal RNA: T $\rightarrow$**G**.
437. 16S ribosomal RNA: A $\rightarrow$**C**.
1430. Lacrimal and jugal bones: (0) not fused, **(1) fused**.
1451. Pterygoid sinus: (0) no expansion into temporal fossa, **(1) expansion into fossa**.
1459. Frontals: supraorbital process/temporal m. attachment: (0) absent, **(1) present**.
1483. Density of bone of posterior process of the tympanic: (0) smooth bone, (1) spiny or irregular edges, **(2) cauliflower like bony growth**, (3) rounded and pachyostotic.
1499. Tuberculum of malleus: (0) large, **(1) minute**.
1515. Nasal passages: (0) separate, **(1) separate until just proximal to the blowhole**, (2) confluent.
1517. Left nasal passage: (0) straight, **(1) U-shaped**.
1519. Melon: (0) small, **(1) large**.
1522. Nasal plug: (0) symmetric, **(1) asymmetric**.
1559. Rostral muscle: (0) absent, **(1) present**.

monophyly, although both provide additional support for monophyly of cetacean families and interfamilial relationships within Odontoceti already supported by both the morphological and DNA sequence data sets. When the restriction-site and myoglobin sequence data sets are combined with the morphological and modified sequence data sets (morphological and restriction-site characters weighted as transversions, myoglobin sequences weighted using PROTPARS step matrix), the results obtained are remarkably similar to those obtained without the myoglobin and restriction site data (see Fig. 8). The 50% majority-rule bootstrap consensus trees are identical, and only 5 of 17 ingroup nodes receive alternative bootstrap values (bootstrap values at three nodes differ by 1%, the value at one node differs by 2%, and the value at one node differs by 4%). Our interpretation of this finding is

that the currently available myoglobin and restriction-site data add little to the debate over odontocete monophyly.

Likelihood-Ratio Test of the Molecular Clock Assumption

The results of the likelihood-ratio test strongly reject the assumption of a molecular clock for the DNA sequence data. The optimal log-likelihood value given every possible alternative rooting position of the Milinkovitch tree (with their data set and assumptions) under the constraint of a molecular clock is −6420.794 (logL0), whereas the best observed log-likelihood value without a molecular clock constraint is −6395.551 (logL1). Assuming that the likelihood-ratio test statistic is χ^2 distributed, we expect that the solution to the equation 2(logL1 – logL0) with 19 degrees of freedom will be 19. The observed value of 50.486 indicates that the molecular clock can be rejected with a probability of $P = 0.0001$. Although we assume it is possible to reject the null hypothesis when nucleotide substitutions have occurred at a constant rate on all but one or a few branches of the tree, the phylograms presented in Figure 10 indicate that in this case, the assumption of a molecular clock affects branch lengths throughout the tree.

Discussion

Phylogenetic Analyses

Phylogenetic analysis of the morphological data set produces an estimate of cetacean relationships that is consistent with the traditional hypothesis of odontocete (toothed whale) monophyly. Indeed, 23 unambiguous synapomorphies support this relationship. This phylogenetic estimate contradicts the novel phylogenetic hypothesis of Milinkovitch et al. (1993, 1994, 1996) in which baleen whales (Mysticeti) were found to be the sister group of the odontocete sperm whales (Physeteridae). This seemingly contradictory set of results is largely a consequence of alternative rooting positions of highly congruent unrooted trees, leading to the following two questions: (1) Is there significant conflict between the molecular and morphological rooting positions? (2) Is a combined-data analysis appropriate and, if so, would it provide a better supported estimate of cetacean phylogeny than either the molecular or morphological data alone?

Two sets of analyses were performed that explored the issue of conflict between the molecular and morphological rooting positions. The outgroup-sampling analysis demonstrated that the rooting position with the molecular data is sensitive to choice of outgroup taxa, whereas the rooting position with the morphological data set is not. Although this result suggests that the molecular rooting position is not robust, it cannot be taken as evidence that the molecular data do not significantly reject the morphological rooting position (and odontocete monophyly). The results of the Templeton test indicate that the Milinkovitch sequence data reject odontocete monophyly, but the modified sequence data do not. As expected, the morphological data set strongly rejects baleen/sperm whale monophyly.

We performed partition-homogeneity tests (Farris et al., 1995) to evaluate levels of heterogeneity between the morphological and molecular data sets. In analyses comparing the modified sequence data set with the morphological data set, the test could not reject data-set homogeneity. However, when the Milinkovitch and morphological data sets are considered, the test indicates significant data-set incongruence. It appears that the Milinkovitch assumptions regarding treatment of the ambiguously aligned gap regions are responsible for this result. The findings of the partition-homogeneity tests (and Templeton tests), indicating that the Milinkovitch sequence data are less congruent with the morphological data than are the modified sequence data, illustrate just how important the treatment of the gap regions (and possibly the choice of outgroup taxa) is to this analysis. Despite the rejection of data-set homogeneity when considering the Milinkovitch and morphological data sets, we proceeded with combined-data phylogenetic analyses with each data set combination to explore how results obtained from analysis

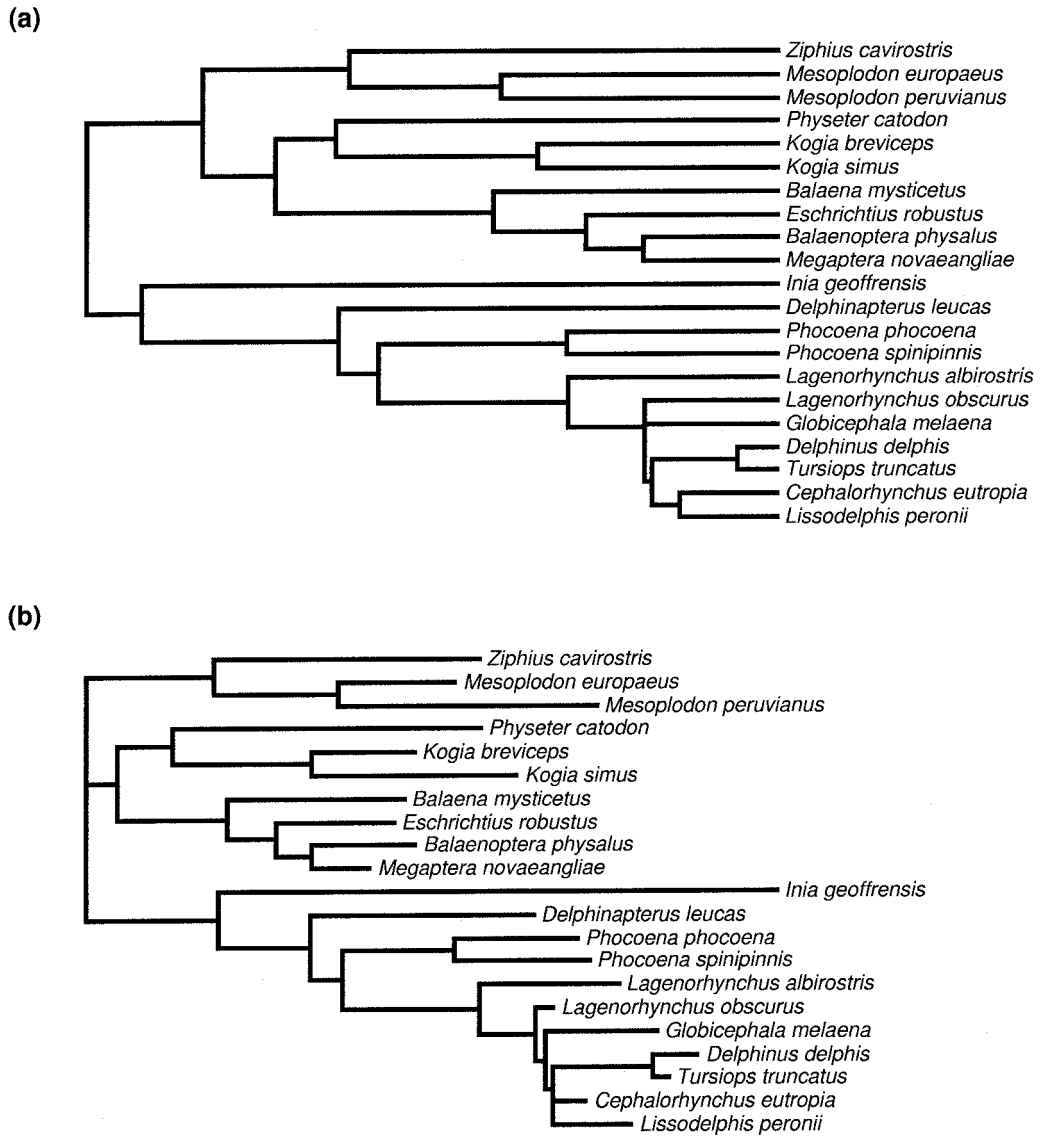

FIGURE 10. Phylograms obtained in the maximum-likelihood analysis of the Milinkovitch data set. The HKY85 model of DNA substitution was assumed in the analysis with the following maximum-likelihood settings: nucleotide frequencies estimated from the data, number of substitution types = 2, rate heterogeneity assumed to follow a gamma distribution with the shape parameter estimated via maximum likelihood, and the transition/transversion ratio estimated via maximum likelihood. A likelihood-ratio test rejected the assumption of a molecular clock with these data ($P = 0.0001$). (a) Molecular clock constraint enforced, tree rooted, log-likelihood score = −6,420.794. (b) No molecular clock constraint, unrooted tree, log-likelihood score = −6,395.550.

of the incongruent data sets would compare with our other combined-data results.

The four combined analyses of the molecular and morphological data resulted in mutually congruent and well-resolved estimates of cetacean phylogenetic relationships (Figs. 8, 9). Aside from differing amounts of resolution within Delphinidae and alternative outgroup topologies, the strict consensus trees obtained in the four

combined analyses were identical. This result indicates that our best supported tree is insensitive to alternative treatments of the sequence data or to the weighting of morphological characters equivalently with transitions or transversions (although degree of support is sensitive to these assumptions). Not unexpectedly, given the large number of morphological characters supporting odontocete monophyly and the instability of the molecular root, the rooting position of the combined-data trees is identical to that of the morphology-only tree. Most other aspects of the combined tree are also consistent with the morphology-only tree, as the unrooted molecular and morphological trees are very similar.

Examination of the combined-data bootstrap results is instructive in several ways. In all of our combined-data analyses, bootstrap support for the combined-data trees increased over that of both the morphology-only and DNA sequence-only trees at nearly every node, especially those that were relatively weakly supported with morphological or molecular data alone (Figs. 8, 9). With the combined data, virtually every node on the tree is strongly supported and bootstrap values of 98–100% represent 12–15 nodes, depending on the data-set combination. These results indicate substantial agreement between the morphological and molecular data sets regarding cetacean phylogeny.

Three of our four data-set combinations indicate robust support for odontocete monophyly with corresponding bootstrap values of 99% or 100% representing this node. However, one of our combined-data analyses (the morphological + Milinkovitch data set with morphological characters weighted equivalently with transitions) resulted in a bootstrap value of 85% at the odontocete node (Fig. 9), a bootstrap value that is substantially smaller than that observed with morphological data alone. This finding is consistent with the results of the Templeton and partition-homogeneity tests in that the Milinkovitch data are found to be in greater conflict with odontocete monophyly than are the modified sequence data. The analyses of the morphology + modified sequence data result in very strong bootstrap support for odontocete monophyly, whether the morphological characters are weighted equivalently with transversions or transitions. This result indicates that the modified sequence data, which do not directly support odontocete monophyly, nevertheless are not in substantial conflict with this grouping. When the morphological data are combined with the Milinkovitch data and morphological characters are weighted equivalently with transversions, the morphological characters overwhelm the conflicting sequence characters such that the bootstrap support for Odontoceti remains at 100%. When the morphological characters are weighted equivalently with transitions, the morphological data still overwhelm the molecular characters conflicting with odontocete monophyly, but this domination is less complete and the bootstrap support for this node falls to 85%.

How should we interpret this finding? We argue that the ambiguously aligned gap regions in the 12S and 16S sequences should be excluded from consideration in the phylogenetic analysis, especially given that the resulting phylogenetic estimate is sensitive to alternative alignments or exclusion of these regions. Although we are less concerned about number of outgroup taxa employed than we are about the treatment of ambiguously aligned gap regions, we also believe that incorporating five outgroup taxa is preferable to the use of three outgroup species by Milinkovitch et al. (1994) because of the potential benefits of shortening the branch connecting cetaceans and extant artiodactyls (Felsenstein, 1978; Hendy and Penny, 1989). Therefore, we believe that the modified treatment of the sequence data is more appropriate than the Milinkovitch treatment and that the combined analyses of the modified and morphological data sets provide a more rigorous estimate of cetacean phylogeny than do the analyses combining the Milinkovitch and morphological data. The phylogenetic implications of this conclusion are inconsequential, however, as the topology of the cetacean phylogenetic estimate is largely unaffected by the alter-

native treatments of the sequence data. Despite our strong conclusions regarding the most appropriate treatment of the data for this analysis, we are not suggesting that this is the final word in the odontocete monophyly debate, only that the data presented thus far are more consistent with the traditional hypothesis than with sperm whale/baleen whale monophyly.

Whether or not one accepts our alternative treatment of the sequence data, a number of important cetacean clades are very strongly supported (Figs. 8, 9). Indeed, in all four of our combined-data analyses, all higher level relationships except the Phocoenidae (porpoises) + Delphinidae (dolphins) clade, the clade including all odontocetes except Physeteridae, and the odontocete clade are very strongly supported in the combined analyses (bootstrap values greater than or equal to 98%). Two of the three nodes that are relatively ''weakly'' supported in comparison with the remaining nodes are nevertheless represented by bootstrap values of ≥70%, and the Odontoceti node is supported by a bootstrap value of 85% in the one analysis in which it is not supported by a bootstrap value of 99% or 100%. Hillis and Bull (1993) found that bootstrap proportions under a wide variety of conditions are conservative estimates of accuracy with bootstrap values of ≥70% corresponding to a probability of ≥95% that the clade is real. Thus, with the possible exception of the Phocoenidae + Delphinidae node, even the relatively weakly supported nodes on our strict consensus trees may be interpreted as strongly supported.

Although the issue of toothed-whale monophyly has recently held center stage in cetacean systematics, there are several additional systematic issues that have long been controversial, and our data shed light on some of these problematic groups as well. For example, the question of the monophyly and phylogenetic placement of river dolphins in relation to other toothed whales has received much attention in the cetacean literature (e.g., Eschricht, 1852; Gray, 1863; Flower, 1867; Miller, 1918; Winge, 1921; Kellogg, 1928; Slijper, 1936; Simpson, 1945; Kasuya, 1973; Rice, 1977; Zhou, 1982; Fordyce, 1983; Muizon, 1984, 1985; Barnes, 1985; Heyning, 1989). River dolphins have widely disjunct distributions, with one species (*Platanista gangetica*) in the Indus and Ganges rivers of India and Pakistan, a second species (*Lipotes vexillifer*) native to the Yangtze River of China, a third species (*Inia geoffrensis*) present in the Amazon River basin, and a fourth species (*Pontoporia blainvillei*) in the estuary of the La Plata River of Argentina and in nearshore waters along the coast of Argentina and Brazil. We have morphological data for each of these species, and our analyses (Figs. 1, 2) indicate that river dolphins as a group are paraphyletic. However, there is strong support for the sister-taxon relationship of the Amazon and La Plata river dolphins (*Inia geoffrensis* and *Pontoporia blainvillei*, respectively). The river dolphins are each placed outside of Delphinoidea (true dolphins, porpoises, narwhales, and belugas), but all are more closely related to Delphinoidea than to Ziphiidae (beaked whales) or Physeteridae (Fig. 1).

Another taxonomic issue that remains controversial is the phylogenetic position of *Orcaella brevirostris*. This species traditionally has been grouped with Delphinidae (true dolphins), but several authors (Kasuya, 1973; Barnes et al., 1985; Lint et al., 1990) have suggested that it may be more closely related to Monodontidae (narwhales and belugas) than to delphinids. Arnason and Gullberg (1996) presented cytochrome *b* data supporting the placement of *O. brevirostris* within Delphinidae and our data agree with this finding. However, the morphological data suggest that *O. brevirostris* is the sister taxon to the remaining species of Delphinidae (Figs. 1, 2) rather than nested within the delphinid lineage.

Molecular Clock

Our analysis strongly rejects the assumption of a molecular clock with these DNA sequence data ($P = 0.0001$; Fig. 10). Several authors (Schlötterer et al., 1991; Milinkovitch et al., 1993, 1994; Milinkovitch, 1995; Arnason and Gullberg, 1996;

Smith et al., 1996) have attempted to estimate divergence times of cetacean lineages using sequence divergence values and an assumed molecular clock. Even if we make the assumption that substitutions occur in a clock-like manner (which the likelihood-ratio test rejects), there are additional problems with the molecular clock hypothesis that the authors have not addressed. Our primary concern is that the authors have failed to present confidence intervals for their estimates of time since divergence (Hillis et al., 1996). Hillis et al. (1996) indicate that in many cases, confidence intervals are so large that estimates of time since divergence are essentially uninformative. Thus, we calculated 95% confidence intervals for the estimates of time since divergence for sperm and baleen whales presented by Milinkovitch et al. (1994). The authors used two molecular clocks, one based on 12S + 16S total substitutions and a second employing third-position cytochrome *b* transversions, both of which were calibrated according to a single point estimate of delphinoid age (monodontids, phocoenids, and delphinids are all known from Miocene deposits dating to possibly 11 million years [MY]; Barnes et al., 1985) rather than from a regression calculation based on multiple data points. Because only a single calibration point was used, the confidence limits of the rate equation cannot be calculated. However, if we are willing to accept a suite of unrealistic assumptions, we can produce minimum confidence intervals for estimates of time since divergence based on the accumulation of substitutions as a Poisson process (the basis of all molecular clock models; Hillis et al., 1996). We must assume that nucleotide substitutions occur as a linear function of time, rate of change is equal across all positions and across all lineages, the true phylogeny is known, the number of substitutions along each branch of the tree can be reconstructed without error, calibration of the clock is performed without error, and regression of time on number of substitutions can be calculated without error. The molecular clock estimate provided by Milinkovitch et al. (1994) for the time since divergence of baleen and sperm whales was 18–19 MY. The minimum 95% confidence interval for this estimate is 13–23 MY for the 12S + 16S clock and 13–27 MY for the cytochrome *b* clock. We emphasize that the confidence intervals will increase with any violation of the assumptions just outlined, and we have already demonstrated with the likelihood-ratio test that nucleotide substitutions have not occurred as a linear function of time and the rate of change has not been equal across all lineages. Furthermore, the estimated divergence times, including the confidence intervals, must be shifted to an earlier window of time if delphinoids diverged earlier than 11 MYA (which seems likely if all three lineages were already present at this time).

Given that the likelihood ratio test strongly rejects the presumption that nucleotide substitutions occur in a clock-like manner, that the calibration of the clock is based on a single point estimate with broad confidence intervals, and that the date used to calibrate the clock is imprecise, we conclude that the use of a hypothesized molecular clock by Milinkovitch et al. (1993, 1994) and Milinkovitch (1995), both in terms of predicting time since divergence and in speculating about rates of morphological evolution, is inappropriate and adds little to the discussion of cetacean evolution.

Rooting Phylogenetic Trees

This study reestablishes the importance of rooting position in phylogenetic analysis. Milinkovitch (1995) correctly recognized that the novel Milinkovitch et al. (1993, 1994) estimate of cetacean relationships differed from the traditional hypothesis only in the rooting position of their tree. Nevertheless, these authors did not assess whether their data set rejected the traditional rooting position before proceeding with a reinterpretation of cetacean morphological character evolution (Milinkovitch et al., 1994; Milinkovitch, 1995). Although it will not always be feasible to test new phylogenetic estimates with alternative data sets as done here, we suggest that

tests such as the Templeton test or parametric bootstrap analysis (Efron, 1982; Bull et al., 1993; Huelsenbeck et al., 1996a) be applied when conclusions regarding character evolution, biogeography, or taxonomic treatment (to list but three of many possible examples) are dependent on the rooting position of a phylogenetic estimate. In this case, taxonomic revision and a reinterpretation of morphological and life history characters in order that they be reconciled with sperm + baleen whale monophyly clearly are premature.

Data Availability

A complete data matrix including morphological, restriction-site, myoglobin amino acid sequence, and DNA sequence data (''modified'' treatment) is available via the Systematic Biology web site and in TreeBASE (http://phylogeny.harvard.edu/treebase).

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APPENDIX 1
MUSEUM SPECIMENS EXAMINED

Osteological specimens examined in this study were from the following United States museums: American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), San Diego Natural History Museum (SDNHM), United States National Museum of Natural History (USNM), and the Texas Memorial Museum (TNHC) at the University of Texas at Austin. For species used in the analyses but not listed in this appendix, character states were coded from character descriptions in the literature.

Tayassua tajacu (2): TNHC 1942, TNHC no number.
Bos taurus (1): TNHC no number.
Antilocapra americana (1): TNHC 236.
Physeter catodon (5): AMNH 34872, 80206; USNM 35315, 253051, 395398.
Kogia breviceps (36): AMNH 36595; SDNHM 20046, 20139, 22489; USNM 22015, 22016, 22893, 283625, 395700, 395734, 504147, 504318, 504338, 504519, 504735, 504747, 504860, 504866, 504902, 504921, 504968, 504992, 550072, 550103, 550128, 550147, 550361, 550396, 550477, 550484, 550486–550488, 550492, 550934, 550991.
Kogia simus (20): SDNHM 16635; USNM 21627, 304512, 484913, 484981, 500357, 504132, 504221, 504336, 504518, 504728, 504749, 504759, 504858, 504968, 550345, 550471, 550482, 550486, 550935.
Tasmacetus shepherdi (1): USNM 484878.
Ziphius cavirostris (8): AMNH 40015; CAS 22592; SDNHM 19557, 21198; USNM 22874, 194514, 550734, 550803.
Berardius bairdii (1): USNM 142118.
Hyperoodon ampullatus (1): USNM 14449.
Mesoplodon bidens (3): USNM 504146, 550204, 550414.
Mesoplodon carlhubbsi (7): CAS 9833, 13505, 21429, 21684; USNM 274591, 504128, 504138.
Mesoplodon densirostris (13): CAS 21136, 22924; USNM 239169, 484996, 486173, 504217, 504950, 550338, 550452, 550746, 550754, 550951, 550952.
Mesoplodon europaeus (20): USNM 23346, 303836, 304738, 306302, 336328, 360854, 504256, 504349, 504473, 504938, 550018, 550069, 550105, 550362, 550390, 550404, 550451, 550483, 550824, 550853.
Mesoplodon ginkgodens (1): USNM 298237.
Mesoplodon grayi (2): USNM 49880, 550149.
Mesoplodon hectori (2): USNM 504260, 504853.
Mesoplodon layardii (1): USNM 550150.
Mesoplodon mirus (4): USNM 504612, 504724, 504764, 550351.
Mesoplodon stejnegeri (7): CAS 16596; USNM 286826, 504882, 504330, 504331, 504345, 571033.
Platanista gangetica (5): AMNH 8461; ANSP 2539; CAS 16340; USNM 23456, 172409.
Inia geoffrensis (15): AMNH 29101, 93414, 93415, 290106; SDNHM 16007, 22836; USNM 49582, 239663, 239667, 395415, 395416, 395602, 395614, 396166, 406801.
Pontoporia blainvillei (36): AMNH 205922, 235271; CAS 15257; USNM RLB 885, 49432, 395674, 482705–

482721, 482724–482727, 482729, 482731, 482732, 482746, 482754, 501127, 501176, 501186, 504920.
Lipotes vexillifer (2): AMNH 57333; USNM 218293.
Monodon monoceros (4): USNM 267958–267961.
Delphinapterus leucas (32): CAS 9802, 10165; SDNHM 20046, 22870; USNM 7382, 7535–7537, 9669, 15446, 16442, 16443, 16485, 21051, 21052, 22207, 22208, 22433, 23208, 24225, 238104–238106, 270085, 275056, 275068, 275075, 305071, 485826, 504673, 504767, 571021.
Phocoena phocoena (114): AMNH 10182, 21514; CAS 5526, 5564, 5573, 7572, 10591, 10592, 11037, 13930, 13931, 14920, 15253, 15258, 15281, 15655, 15671, 15944, 15948, 15949, 15987, 15992, 15993, 16109, 16112, 16179, 16572, 16602, 16603, 16609, 16629, 16630, 16633, 16634, 16668, 16749, 21380, 21381, 21383–21386, 21493, 21495, 21496, 21505, 21506, 21508, 21706, 21748, 21757, 21760, 22181, 22196, 22200, 22202, 22205–22211, 22224, 22259, 22270, 22271, 22173, 22538, 22546, 22547, 22558, 22559, 22567, 22580–22582, 22622, 22633, 22774, 22826, 22827, 22950, 22951, 22968, 22973, 22987, 22998; USNM 13305, 13306, 16610, 22555, 83871, 83990, 49428, 49564, 217912, 218739, 218740, 270985, 274783, 274588–274590, 484975, 504105, 504120, 504588, 504596, 504600, 550152, 550189, 550191, 550312.
Phocoena spinipinnis (25): USNM 299994, 395376, 395379, 395627, 395628, 395736–395739, 395744–395746, 395752, 395753, 550233, 550234, 550246, 550247, 550264, 550266, 550275, 550276, 550278, 550283, 550284.
Phocoena sinus (5): SDNHM 20688; USNM 303308, 395722, 395723, 395892.
Neophocaena phocaenoides (11): AMNH 57330; USNM 49544, 239990, 240001–240003, 240862, 241503, 504910, 550473, 550489.
Phocoenoides dalli (44): AMNH 128104; CAS 6237, 9885, 9886, 12770, 15278, 15280, 15983, 16604, 16008, 16297, 16626, 22564, 22584, 22839, 22949, 22967; SDNHM 23019; USNM 22556, 219334, 238083, 244234, 251757, 276063–276065, 276394, 284794, 286863, 286867, 286868, 286870, 286871, 286874, 286877–286881, 286884, 286889, 286890, 290627, 298238.
Feresa attenuata (10): SDNHM 21561; USNM 267574, 395177, 484995, 504916–504919, 550346, 550389.
Orcaella brevirostris (4): USNM 199743, 284429, 284430, 486170.
Pseudorca crassidens (12): CAS 13338, 13339, 13888, 16465; USNM 11320, 20932, 23282, 218360, 219325, 484982, 485827, 501200.
Sousa chinensis (2): USNM 21499, 258859.
Sousa plumbea (3): USNM 550939–550941.
Sotalia fluviatilis (4): CAS 13947, 16658; USNM 21499, 253476.
Steno bredanensis (33): CAS 9061, 12889, 16451, 16452, 16624, 16625; USNM 4121, 21169, 49628, 49983, 282317, 339862, 364532, 395770, 395772, 470542–470544, 504461, 504462, 504464, 504479, 504486–504488, 504493, 504495, 504496, 504498, 504499, 550180, 550218, 550343.
Orcinus orca (13): CAS 5574, 16464, 20749; USNM 11980, 16487, 16488, 21330, 22068, 23004, 37166, 238122, 239357, 550857.
Globicephala melaena (26): CAS 8055, 12764, 12890, 13462, 16466, 21135, 21217; SDNHM 20065, 21268; USNM 20958, 21118, 259706, 303018, 395357–395365, 395372, 395373, 484974, 504593.
Globicephala macrorhynchus (7): CAS 22825; USNM 9076, 22570–22572, 37261–37263.
Stenella clymene (24): USNM 504408, 550498–550500, 550505–550508, 550514–550517, 550521–550523, 550525, 550526, 550528–550533, 550535, 550539.
Stenella longirostris (35): CAS 10529, 15665–15669, 16455–16458; USNM 21168, 23302, 49661, 88976, 112832, 291352, 291958, 324974, 395269–395274, 395404, 395409, 395411–395414, 395593, 395599, 395930–395932.
Stenella frontalis (7): CAS 16642; USNM 550376, 550748, 550800, 571012, 571139, 571244.
Stenella attenuata (29): CAS 16453, 16454; USNM 218344, 254671, 258641, 259311, 261427–261430, 339648, 347651, 395264, 395265, 395386–395389, 395394, 395395, 395397, 395407, 395608, 395610, 470562, 550016, 550017, 550356, 550374.
Stenella coeruleoalba (25): CAS 16720, 21749, 22178, 22563, 22922; USNM 504341, 504350, 504426–504429, 504522, 504523, 504760, 504819, 504822, 504829–504832, 504867–504869, 504880, 504885.
Grampus griseus (18): CAS 13461, 21218; SDNHM 21554; USNM 16486, 22448, 49347, 49895, 501199, 504126, 504328, 504852, 504942, 550391–550393, 550752, 550794, 550936.
Tursiops truncatus (48): AMNH 74485; CAS 9884, 10464, 10465, 10474, 12738, 13937, 14935, 15683, 15685–15687, 15996, 15997, 16183, 16281–16284, 16459–16463, 22280, 22583; SDNHM 21403; USNM 11993, 11994, 241375, 252100, 252101, 252104, 252105, 305767, 307545, 395381, 550395, 550436, 550454, 550455, 550493, 550736, 550747, 550795, 550820, 550829, 550883.
Delphinus delphis (86): CAS 1154, 13334–13337, 13886, 13887, 13936, 15249, 15674–15682, 15684, 16242, 16248, 16250–16280, 16336, 16647, 16662, 21037, 21150, 21374, 21437, 22149, 22577, 22625, 22946, 22947; SDNHM 23017, 23018; USNM 487769, 487770, 487773, 487774, 487777–487780, 487807, 487809, 487810, 487812, 487815, 487817–487820, 500287, 500289, 500295.
Lagenorhynchus acutus (23): USNM 14228–14231, 14234–14237, 14242–14245, 14250, 14251, 14255–14258, 14263, 14264, 22934, 22942, 20960.
Lagenorhynchus australis (9): USNM 395344–395351, 395354.
Peponocephala electra (18): USNM 395785, 504250, 504502–504508, 504510–504517, 504948.
Lagenorhynchus obscurus (21): SDNHM 21167; USNM 550264, 550742–550745, 550757–550764, 550766–550770, 550796, 550831.
Lagenorhynchus obliquidens (47): CAS 12189, 13240, 13488, 13492, 13683, 13924, 13948, 16159, 16593, 16632, 16652, 16663, 16748, 21378, 21379, 21431, 21487, 21703, 22258, 22587; SDNHM 21215, 21216, 21219, 21222; USNM 15256, 63299, 112978, 270980,

274627, 274922, 286862, 290512, 290628–290636, 290641, 290647, 290648, 395869, 395872, 504293.

Lagenorhynchus albirostris (15): USNM 35156, 49753, 267573, 504628–504630, 504659, 504660, 504769, 504924, 550208, 550222–550224, 550352.

Lagenodelphis hosei (4): SDNHM 22942; USNM 396079, 504411, 550022.

Lissodelphis borealis (19): CAS 16243, 16623, 16664; SDNHM 22942; USNM 8160, 270981, 286872, 286882, 286883, 290625, 290626, 395767, 484929, 550026, 550027, 550071, 550188, 550917, 550922.

Lissodelphis peroni (1): USNM 501198.

Cephalorhynchus commersoni (9): USNM 252568, 395353, 484889, 504072, 504073, 550154–550156, 550449.

Cephalorhynchus hectori (2): USNM 84588, 500864.

Cephalorhynchus eutropia (4): USNM 21167, 395374, 395375, 395625.

Cephalorhynchus heavisidii (1): USNM 550067.

APPENDIX 2
CHARACTER LIST

The following character list includes all of the osteological characters (informative or uninformative), as well as 54 soft tissue characters taken from the literature. Mead (1975), Heyning (1989), and Heyning and Mead (1990) were the primary literature sources for descriptions of the soft tissue characters in the cranial region, especially the nasal passage complex (characters 1508–1560). Characters 1581–1602 came from the following literature sources: Kellogg (1928), Slijper (1936), Tomilin (1957), Van Valen (1968), Barnes and Mitchell (1978), Zhou (1982), Barnes (1984), Fordyce (1985), Heyning and Mead (1990), and Thewissen (1994). Otherwise, citations providing the literature source(s) in which each character was discussed follow the character state designation.

1398. Facial plane (dorsal surface in profile): (0) concave, (1) flat to convex (Heyning, 1989).
1399. Cranial vertex (elevated region of skull posterior to bony nares): (0) symmetric, (1) asymmetric (Muizon, 1988; Heyning, 1989).
1400. Supracranial basin: (0) absent, (1) present (Abel, 1905; Heyning, 1989; Muizon, 1991).
1401. Prenarial basin: (0) absent, (1) present (True, 1910; Mead, 1975; Heyning, 1989; Muizon, 1991).
1402. Premaxillae: (0) symmetric, (1) asymmetric.
1403. Premaxillae: (0) left premaxilla lies lateral to left narial opening, (1) left premaxilla enters left narial opening.
1404. Premaxillae: (0) do not contribute to vertex of skull, (1) contribute to vertex (Moore, 1968; Heyning, 1989; Muizon, 1991).
1405. Premaxillae: (0) dorsomedial surfaces of premaxillae do not meet, (1) dorsomedial surfaces of premaxillae meet (Muizon, 1988).
1406. Premaxillae: (0) thin and plate-like over entire length, (1) thin and plate-like anteriorly, but greatly thickened along posterior ascending process (Moore, 1968).
1407. Premaxillae: (0) not displaced laterally from narial fossa, (1) displaced laterally from narial fossa (Muizon, 1988; Heyning, 1989).
1408. Premaxillae: (0) no reduction of posterior edge of ascending processes, (1) reduction of posterior edge of ascending processes, (2) only left posterior edge of process reduced (Muizon, 1984, 1988; Heyning, 1989).
1409. Premaxillae (at vertex of skull): (0) do not project more anteriorly than nasals, (1) right premaxilla projects more anteriorly than nasals, (2) both premaxillae project more anteriorly than nasals (Moore, 1968).
1410. Ascending processes of premaxillae: (0) bosses absent, (1) bosses present (Flower, 1867; Muizon, 1988; Heyning, 1989).
1411. Premaxillary sac fossae: (0) present, (1) absent (Heyning, 1989).
1412. Premaxillary artery grooves: (0) posterolateral groove does not extend length of premaxilla, (1) posterolateral groove does extend length of premaxilla (Muizon, 1988).
1413. Premaxillary foramen: (0) absent, (1) present.
1414. Premaxillary foramen: (0) round, (2) laterally compressed (Muizon, 1984).
1415. Premaxillary foramen size: (0) right and left equal, (1) left much larger than right.
1416. Premaxillary crest: (0) absent, (1) present (Moore, 1968).
1417. Posterior extremity of premaxillae on synvertex: (0) not angled inward (faces anteriorly), (1) angled inward (faces medially) (Moore, 1968; Muizon, 1991).
1418. Maxillary–premaxillary suture along rostrum: (0) separate, (1) fused.
1419. Maxillae: (0) abut supraorbital processes of frontal, (1) overlay supraorbital process of frontal (Miller, 1923; Muizon, 1984, 1991; Heyning, 1989).
1420. Maxillae: (0) no crest, (1) low crest forms on supraorbital process (Muizon, 1984; Barnes, 1985).
1421. Maxillae: (0) no crest, (1) pneumatic maxillary crest present (Zhou, 1982; Muizon, 1984, 1987; Heyning, 1989).
1422. Medial maxillary processes: (0) absent, (1) present (Muizon, 1984, 1988).
1423. Facial depression for insertion of maxillonasolabialis muscle on maxillae: (0) absent, (1) present (Mead, 1975).
1424. Rostral portion of maxillae: (0) not constricted at proximal base, (1) constricted at proximal base (Muizon, 1984; Barnes, 1985).
1425. Antorbital tubercle (= maxillary tubercle): (0) absent, (1) present (Moore, 1963; Heyning, 1989).
1426. Antorbital notch at base of rostrum: (0) absent, (1) present (Moore, 1963; Heyning, 1989).
1427. Antorbital process at base of rostrum: (0) lies along lateral edge of cranium, (1) lies within supracranial basin (Muizon, 1991).
1428. Vomer: (0) exposed between maxillae on palate, (1) not exposed between maxillae on palate (Zhou, 1982).

1429. Mesorostral canal: (0) not ossified, (1) ossified (Moore, 1963; Heyning, 1989).
1430. Lacrimal and jugal bones: (0) not fused, (1) fused (Flower, 1869; Schulte, 1917; Heyning, 1989; Muizon, 1991).
1431. Number of nasal bones: (0) 2, (1) 1, (2) 0 (Küzmin, 1977; Heyning, 1989; Muizon, 1991).
1432. Shape of nasals in dorsal view: (0) anteroposteriorly compressed, (1) anteroposteriorly elongate (Muizon, 1988).
1433. Nasal protuberances: (0) absent, (1) present (Muizon, 1988).
1434. Nasals: (0) do not extend as high as frontals, (1) are same height as frontals, (2) raised higher than frontals (Muizon, 1988).
1435. Nasals: (0) right nasal lies between premaxilla in crest, (1) right nasal does not lie between premaxilla in crest (Moore, 1968).
1436. Anterior surface of nasals: (0) incline vertically (flat), (1) incline posteriorly to vertical, (2) incline convex, (3) incline anteriorly to vertical (Moore, 1968).
1437. Narial fossae: (0) do not face ventrolaterally, (1) face ventrolaterally.
1438. Narial fossae: (0) symmetric, (1) left much larger than right.
1439. Palatines: (0) not fused with maxillae, (1) fused with maxillae (Muizon, 1988).
1440. Palatines: (0) not covered by pterygoids, (1) covered by pterygoids (Muizon, 1987).
1441. Palatines: (0) positioned medially, (1) positioned laterally (Muizon, 1987).
1442. Palatine grooves: (0) absent, (1) present (Muizon, 1984).
1443. Lateral plates of palatines: (0) absent, (1) present (Muizon, 1984, 1988, 1991).
1444. Lateral plates of palatines: (0) do not form bony bridge over orbit, (1) form bony bridge over orbit (Muizon, 1984).
1445. Pterygoids: (0) meet at midline, (1) widely separated (Flower, 1883; Marsh et al., 1989).
1446. Lateral plate of pterygoids: (0) present, (1) absent (Kellogg, 1936; Fraser and Purves, 1960; Zhou, 1982; Muizon, 1984, 1991).
1447. Pterygoid hamuli: (0) small, (1) large (Heyning, 1989; Muizon, 1991).
1448. Lateral plates of pterygoid hamuli: (0) absent, (1) present (Muizon, 1984).
1449. Pterygoid hamuli: (0) have smooth ventral surface, (1) have ventral keels (Muizon, 1988).
1450. Pterygoid hamuli: (0) meet at midline, (1) separated.
1451. Pterygoid sinus: (0) does not expand into temporal fossa, (1) expands into temporal fossa (Muizon, 1991).
1452. Pre- and postorbital lobes of the pterygoid sinus: (0) absent, (1) present (Muizon, 1988; Heyning, 1989).
1453. Temporal fossa: (0) not roofed over by lateral expansion of the maxillae, (1) roofed over by lateral expansion of the maxillae (Muizon, 1988; Heyning, 1989).
1454. Mesethmoid: (0) not expanded posterodorsally, (1) expanded posterodorsally (Muizon, 1984, 1988).
1455. Mesethmoid: (0) roofed over by nasals, (1) exposed dorsally (Miller, 1923).
1456. Ethmoturbinal bones: (0) present, (1) absent (Yablokov, 1964).
1457. Exposed surface of frontals: (0) greater than area of nasals, (1) less than or equal to area of nasals (Muizon, 1988).
1458. Supraorbital processes of frontals: (0) not raised dorsally, (1) raised dorsally, (2) angled ventrally and greatly elongated (Muizon, 1988).
1459. Supraorbital processes of frontals: (0) no temporal muscle attachment, (1) temporal muscle attachment (Mead, 1975).
1460. Frontals: (0) not excavated by air sinus, (1) excavated by air sinus (Muizon, 1984, 1988; Heyning, 1989).
1461. Frontal protuberance on vertex: (0) absent, (1) present (Muizon, 1984, 1988).
1462. Spiny process of the squamosal: (0) absent, (1) present (Muizon, 1987).
1463. Cranial hiatus: (0) absent, (1) present (Heyning, 1989).
1464. Posterior sinus: (0) absent, (1) present (Muizon, 1984, 1991).
1465. Mandibular symphysis: (0) extends less than half of the length of the mandible, (1) extends greater than half of the length of the mandible (Heyning, 1989).
1466. Mandibular symphysis: (0) mandibles fused, (1) mandibles connected by ligaments (Flower, 1885).
1467. Tooth number of upper jaw: (0) 7–11 in each side of each jaw, (1) polydont (>11 teeth/jaw) (2) reduction of teeth (<7 teeth/jaw).
1468. Tooth number of lower jaw: (0) 7–11 in each side of each jaw, (1) polydont (>11 teeth/jaw), (2) reduction of teeth (<7 teeth/jaw).
1469. Tooth enamel: (0) smooth, (1) reticulate, (2) nodular (Zhou, 1982).
1470. Teeth: (0) conical, (1) spatulate, (2) laterally compressed (Moore, 1968; Heyning, 1989).
1471. Teeth: (0) deeply rooted, (1) not deeply rooted (Moore, 1968).
1472. Base of teeth: (0) conical, (1) exhibit annular swelling (Muizon, 1984, 1988).
1473. Accessory shelf on posterior teeth: (0) absent, (1) present (Flower, 1867).
1474. Upper tooth rows: (0) separated and diverged, (1) tightly spaced and run parallel (Zhou, 1982).
1475. Teeth in females: (0) erupt in adulthood, (1) do not erupt in adulthood (Moore, 1968; Hay and Mansfield, 1989).
1476. Teeth in males: (0) oriented vertically, (1) incline posteriorly, (2) incline anteriorly (Moore, 1968).
1477. Enlarged apical mandibular teeth: (0) absent, (1) present (Heyning, 1989; Mead, 1989).
1478. Location of enlarged apical mandibular teeth: (0) apical, (1) on mandibular symphysis, (2) posterior to mandibular symphysis (Mead, 1989).

1479. Denticles on teeth: (0) absent, (1) present (McCann, 1962; Moore, 1968).
1480. Location of denticles on teeth: (0) posterior edge, (1) medial edge, (2) between medial and anterior edge, (3) anterior edge, (4) lateral edge (Moore, 1968).
1481. Tympano-squamosal suture: (0) present, (1) absent (Kasuya, 1973; Muizon, 1984; Heyning, 1989).
1482. Posterior process of the tympanic: (0) equal to or greater in size than tympanic bulla, (1) much smaller in size than tympanic bulla (Kasuya, 1973; Yamada, 1953; Muizon, 1984, 1991; Heyning, 1989).
1483. Density of bone of posterior process of the tympanic: (0) smooth bone, (1) spiny or irregular edges, (2) cauliflower-like bony growth, (3) rounded and pachyostotic (Kasuya, 1973; Heyning, 1989; Muizon, 1991).
1484. Anterior spine of the tympanic: (0) absent, (1) present (Kasuya, 1973; Muizon, 1984, 1987, 1988, 1991).
1485. Lateral furrow of the tympanic: (0) absent, (1) shallow groove, (2) deep, well-defined groove (Kasuya, 1973; Muizon, 1984, 1988).
1486. Sigmoid process of the tympanic directed: (0) anteriorly to anterolaterally, (1) laterally to posterolaterally (Kasuya, 1973).
1487. Involucrum of tympanic: (0) not excavated, (1) excavated (Muizon, 1988).
1488. Involucrum of tympanic: (0) anterior portion not expanded, (1) anterior portion expanded (Muizon, 1991).
1489. Size of bone of anterior process of the periotic: (0) equal to or greater than size of pars cochlea, (1) much smaller than pars cochlea (Kellogg, 1936; Yamada, 1953; Muizon, 1984; Heyning, 1989).
1490. Bony connection between anterior process of the periotic and cranium: (0) present, (1) absent (ligamentous) (Heyning, 1989).
1491. Bony connection between posterior process of the periotic and squamosal/occipital bones: (0) present, (1) absent (ligamentous) (Fraser and Purves, 1960; Kasuya, 1973; Muizon, 1984; Heyning, 1989).
1492. Shape of bone of posterior process of the periotic: (0) robust, (1) thin plate (Kasuya, 1973).
1493. Size of bone of posterior process of the periotic: (0) much larger than pars cochlea, (1) smaller than pars cochlea (Yamada, 1953; Kasuya, 1973; Heyning, 1989).
1494. Articular process of the periotic: (0) absent, (1) present (Muizon, 1987; Messenger, 1994).
1495. Styloid process on the anterior process of the periotic: (0) absent, (1) present (Muizon, 1988).
1496. Epitubarienne fossa: (0) absent, (1) present (Kellogg, 1936; Muizon, 1984, 1988, 1991).
1497. Internal aperture of the fallopian aqueduct: (0) lies within internal auditory meatus, (1) does not lie within internal auditory meatus.
1498. Internal auditory meatus: (0) pyriform, (1) circular (Muizon, 1984).
1499. Tuberculum of malleus: (0) large, such that malleus is elongate, (1) nearly absent, such that the malleus is round (Muizon, 1985, 1991).
1500. Muscular process of the malleus: (0) smaller than the manubrium, (1) larger than the manubrium (Muizon, 1985, 1991).
1501. Cervical vertebrae: (0) unfused, (1) C2–C7 fused (2) C1–C7 fused, (3) C1–C2 fused (De Smet, 1977; Rommel, 1990).
1502. Transverse processes of the lumbar vertebrae: (0) anterior and posterior border run parallel, (1) triangular (Muizon, 1984, 1985, 1988).
1503. Ventrolateral processes of the sternum: (0) absent, (1) present in the form of small raised areas or bumps (2) present as well-developed elongate processes (Klima et al., 1980; Muizon, 1988).
1504. Coracoid process of the scapula: (0) present, (1) absent (True, 1904; Muizon, 1984, 1985, 1987, 1991; Cozzuol, 1989).
1505. Acromion process of the scapula: (0) lies along lateral edge of scapular head, (1) lies along anterior edge of scapular head (Muizon, 1987, 1991).
1506. Deltopectoral tuberosity of humerus: (0) lies at proximal end of humerus, (1) lies midway down the humeral shaft (Muizon, 1988).
1507. Olecranon process of the ulna: (0) present as a distinct process, (1) present as a slightly raised proximal posterior edge, (2) absent (Muizon, 1984).
1508. Panbone in mandible: (0) absent (mandible solid), (1) present.
1509. False gills: (0) absent, (1) present (Leatherwood and Reeves, 1983).
1510. Prenarial basin: (0) not fat filled, (1) fat filled.
1511. Spermaceti organ: (0) absent, (1) present (Norris and Harvey, 1972; Cranford et al., 1996).
1512. Museau de singe: (0) absent, (1) present (Norris, 1964; Cranford et al., 1996).
1513. Throat grooves: (0) absent, (1) present.
1514. Throat groove shape: (0) multiple, parallel, (1) single, V-shaped, (2) irregular in number and shape.
1515. Nasal passages: (0) separate, (1) separate until just proximal to the blowhole, (2) confluent.
1516. Nasal passages: (0) oriented vertically, (1) angled anteriorly.
1517. Left nasal passage: (0) straight, (1) U-shaped.
1518. Melon: (0) absent, (1) present.
1519. Melon: (0) ''small compared to that of odontocetes,'' (2) large (Heyning and Mead, 1990).
1520. Melon: (0) not divided by connective tissue, (1) divided by connective tissue.
1521. Melon: (0) does not extend into right nasal plug, (1) extends into right nasal plug.
1522. Nasal plug: (0) symmetric, (1) asymmetric.
1523. Nasal plug: (0) does not have lateral lips, (1) has lateral lips.
1524. Cartilage in nasal septum: (0) absent, (1) present.
1525. Blowhole shape: (0) comma-shaped openings, (1) transverse crescentic, apices face anteriorly,

(2) transverse crescentic, apices face posteriorly, (3) longitudinal, rectangle, (4) sigmoidally shaped longitudinal slit, (5) transverse crescentic, apices face posteriorly and to the right, (6) longitudinal slit, (7) diagonal V-shaped.
1526. Blowhole location: (0) midpoint of rostrum, (1) apex of rostrum.
1527. Blowhole ligament: (0) absent, (1) present.
1528. Blowhole ligament: (0) not appressed against skull, (1) appressed against skull.
1529. Cartilage in blowhole ligament: (0) absent, (1) present.
1530. Blowhole ligament: (0) not attached to lateral premaxilla, (1) attached to lateral premaxilla.
1531. Proximal sacs (nasal sac): (0) absent, (1) present.
1532. Proximal sacs (nasal sac): (0) modified into frontal sac, (1) modified into inferior vestibule/nasofrontal/posterior nasal sac.
1533. Distal sac (nasal sac): (0) absent, (1) present.
1534. Posterior nasal sacs: (0) absent, (1) present.
1535. Posterior nasal sacs: (0) single, (1) divided.
1536. Nasofrontal sac (anterior section): (0) absent, (1) present.
1537. Nasofrontal sac: (0) anterior sac smooth, (1) anterior sac trabeculate.
1538. Premaxillary sacs (nasal sac): (0) absent, (1) present.
1539. Premaxillary sacs (nasal sac): (0) no diverticula, (1) lateral diverticula in right premaxillary sac.
1540. Premaxillary cleft: (0) not filled with connective tissue and cartilage, (1) filled with connective tissue and cartilage.
1541. Vestibular sac (nasal sac): (0) absent, (1) present.
1542. Vestibular sac (nasal sac): (0) not pigmented, (1) lined with black pigment.
1543. Vestibular sac (nasal sac): (0) floor not rigid, (1) floor rigid.
1544. Vestibular sac (nasal sac): (0) undivided, (1) bilaterally divided.
1545. Vestibular sac (nasal sac): (0) right and left side same size, (1) right side larger.
1546. Vestibular sac (nasal sac): (0) no intrinsic muscle in sac, (1) intrinsic muscle in sac.
1547. Vestibular sac (nasal sac) floor: (0) smooth, (1) wrinkled.
1548. Inferior vestibule: (0) symmetric, (1) asymmetric.
1549. Accessory sacs (nasal sac): (0) absent, (1) present.
1550. Diagonal membrane: (0) absent, (1) present.
1551. Spiracular plate: (0) smooth, (1) rugose.
1552. Spiracular cavity: (0) slitlike, (1) round.
1553. Pars posteroexternus muscle: (0) absent, (1) present.
1554. Pars intermedius muscle: (0) absent, (1) present.
1555. Pars anteroexternus muscle: (0) does not extend over premaxilla, (1) extends over premaxilla.
1556. Pars posterointernus muscle: (0) absent, (1) present.
1557. Pars anterointernus muscle: (0) 1 insertion, (1) 2 insertions.
1558. Vertex muscle: (0) absent, (1) present.
1559. Rostral muscle: (0) absent, (1) present.
1560. Rostral muscle: (0) does not originate from mandible, (1) originates from mandible.
1561. Sexual dimorphism: (0) males larger than females, (1) females larger than males, (2) males and females same size (Leatherwood and Reeves, 1983).
1562. Dorsal fin: (0) absent, (1) present, (2) dorsal hump (Leatherwood and Reeves, 1983).
1563. Maxillae: (0) abut supraorbital process, (1) extend posteriorly beneath supraorbital process (True, 1904; Miller, 1923; McLeod et al., 1993).
1564. Temporal crest: (0) lies at ventral surface of supraorbital process, (1) lies at dorsal surface of supraorbital (McLeod et al., 1993).
1565. Baleen: (0) absent, (1) present.
1566. Palate: (0) narrow with flat ventral surface, (1) wide with prominent ventral keel (True, 1904; McLeod et al., 1993).
1567. Rostrum: (0) straight, (1) transversely compressed and arched slightly dorsoventrally, (2) transversely compressed and extremely arched dorsoventrally (True, 1904; McLeod et al., 1993).
1568. Mandible: (0) mandibular condyle slightly curved and directed posteroventrally, (1) mandibular condyle rounded and directed dorsally (True, 1904; McLeod et al., 1993).
1569. Dentary: (0) narrow and straight, (1) expanded and arched dorsoventrally (True, 1904; McLeod et al., 1993).
1570. Squamosal: (0) glenoid fossa and zygomatic portion of squamosal not expanded ventrally, (1) glenoid fossa and zygomatic portion of squamosal expanded ventrally (True, 1904; McLeod et al., 1993).
1571. Pterygoids: (0) do not reach the basicranium posteriorly, (1) extend posteriorly beneath basicranium (True, 1904; McLeod et al., 1993).
1572. Baleen plates: (0) short (<6% of body length), (1) long (>15% of body length) (True, 1904; McLeod et al., 1993).
1573. Nucleus of lateral olfactory nerve tract: (0) present, (1) absent (Pilleri and Gihr, 1970).
1574. Ribs: (0) first rib not attached to cervical vertebrae, (1) first rib attached to several cervical vertebrae by ligaments (Slijper, 1936; De Smet, 1977).
1575. Manus: (0) pentadactyl, (1) tetradactyl (Yablokov, 1964; Van Valen, 1968).
1576. Sternum: (0) comprised of several bones, (1) comprised of one bone (Yablokov, 1964; Van Valen, 1968).
1577. Sternum: (0) several ribs attach to sternum, (1) one rib attaches to sternum (Yablokov, 1964; Van Valen, 1968).
1578. Tympanic membrane: (0) present in the form of a thin, calcified ligament, (1) present in the form of ''glove finger'' (thickened membrane shaped like finger of glove) (Ketten, 1991).
1579. Tympanic bulla: (0) not attached to mandibular ramus, (1) attached to posterior margin of mandibular ramus with band of fibrous tissue (Ketten, 1991).
1580. Middle ear ossicles: (0) ligamentous attachment

to bulla, (1) fused to bulla and joints stiffened (Ketten, 1991).
1581. Horizontal caudal fluke as the method of propulsion: (0) absent, (1) present.
1582. Flippers as forelimbs: (0) absent, (1) present.
1583. External hind limbs: (0) present, (1) absent.
1584. Sacral segment of the vertebrae: (0) present, (1) absent.
1585. Cervical vertebrae: (0) not compressed, (1) anteroposteriorly compressed.
1586. Haemal arches associated with the caudal vertebrae: (0) absent, (1) present.
1587. Rotational movement in the elbow joint: (0) present, (1) absent.
1588. Middle ear sinus: (0) does not surround region of tympanoperiotic bones, (1) extends into the region around the tympanoperiotic bones.
1589. Mandibular foramen: (0) small, (1) large.
1590. External hair: (0) present, (1) absent or extremely reduced.
1591. Blubber: (0) absent, (1) present.
1592. Gall bladder: (0) present, (1) absent.
1593. True vocal cords: (0) present, (1) absent.
1594. Palatine foramina: (0) present, (1) absent.
1595. Falcate processes of the basioccipital (= basioccipital crests): (0) small, (1) large.
1596. Maxillary foramina (derived from infraorbital foramen): (0) single, (1) multiple.
1597. Vomer: (0) does not extend posteriorly to reach basisphenoid-basioccipital, (1) extends onto basicranium covering basisphenoid-basioccipital.
1598. Number of phalanges: (0) 3, (1) >3.
1599. Eustachian tube: (0) does not enter pterygoid sinus, (1) expanded into pterygoid sinus.
1600. Primary blood supply to brain: (0) by way of internal carotid artery, (1) by way of intravertebral rete mirabile.
1601. External auditory meatus (ear opening): (0) large with clear opening to auditory canal, (1) small and obstructed by dense cerumen or wax.
1602. Body: (0) not fusiform, (1) torpedo shaped or fusiform.
1603. Crus longum of incus: (0) elongate and thin, (1) shortened and greatly inflated such that width approaches length (Thewissen and Hussain, 1993).
1604. Mallear joint of incus: (0) opposite crus longum, (1) rotated 4°, (2) rotated 90° (Thewissen and Hussain, 1993).

APPENDIX 3

Character matrix for the morphological data set. The numbering of the morphological characters begins with 1398 because the 12S, 16S, and cytochrome *b* sequence characters correspond to numbers 1–1397.

	1400	1410	1420	1430	1440	1450
	.	.	.	.	.	.
	<morphological data begin					
B. taurus	1000000001??0 1 0 0 ? ?	0?0000000000? 1 0 0 0 1	00? ? 0000000 ?	1 0	00?1??00
C. dromedarius	0000000000??0 1 ? ? ? ?	0??000000000? 1 0 0 0 1	00? ? 00?0?0? ?	1 0	00?1??00
T. tajacu	1000000000??0 1 ? ? ? ?	0?1000000000? 1 0 0 0 1	00? ? 0010000 ?	1 0	00?1??00
A. americana	1000000000??0 1 0 0 ? ?	0?0000000000? 1 0 0 0 1	00? ? 0000000 ?	1 0	00?1??00
T. napu	0000000000??0 1 0 0 ? ?	0?0000000000? 1 0 0 0 1	00? ? 00?000? ?	1 0	00?1??00
Archaeocete	1000000000??0 1 ? 0 ? ?	0?000007000? 1 0 0 0 1	00? ? 0000000 ?	1 0	00?1??0?
B. mysticetus	1000001000??0 1 0 0 ? ?	0?0000000000? 1 0 0 0 1	01? ? 0000000 ?	1 0	0001??00
E. glacialis	1000000000??0 1 0 0 ? ?	0?0000000000? 1 0 0 0 (01)	01? ? 0000000 ?	1 0	00010000
B. acutorostrata	1000000000??0 1 0 0 ? ?	0?0000000000? 0 0 0 0 1	01? ? 0000000 ?	1 0	00010000
B. physalus	1000000000??0 1 0 0 ? ?	0?0000000000? 0 0 0 0 (01)	01? ? 0000000 ?	1 0	00010000
E. robustus	1000000000??0 1 0 0 ? ?	0?0000000001? 0 0 0 0 1	01? ? 0000000 ?	1 0	00010000
M. novaeangliae	1000000000??0 1 0 0 ? ?	0?0000000000? 0 0 0 0 1	01? ? 0000000 ?	1 0	00010000
P. catodon	0110110000??0 1 0 1 0 1	0?0100010010 0 0 (01) 1 0	00? ? 0100000 ?	0 1	00001000
K. breviceps	0110110000??0 1 0 1 0 1	0?0100010011 0 0 1 2 ?	??? ? 0100000 ?	0 1	00001000
K. simus	0110110000??0 1 0 1 0 1	0?0100010011 0 0 1 2 ?	??? ? 0100000 ?	0 1	00001000
Z. cavirostris	0101101010000 0 0 1 0 (01)	11110001001?(01) 1 0 0 1	020 2 0000000 ?	0 1	10001010
B. bairdii	0100101000000 0 0 1 0 0	10010001001?(01) (01) 0 0 0	020 (12) 0000000 ?	0 1	10001010
H. planifrons	0100101010020 0 0 1 0 0	10110001001?(01) 0 0 0 0	021 3 0000000 ?	0 1	10001010
T. shepherdi	0100001010010 0 0 1 0 0	10110001001?(01) 0 0 0 0	020 0 0000000 ?	0 1	10001010
M. densirostris	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. bidens	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. europaeus	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. peruvianus	0100101010020 0 0 1 0 0	11110001001? 1 1 0 0 0	010 ? 0000000 ?	0 1	10001010
M. mirus	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. layardii	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. grayi	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. hectori	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. ginkgodens	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. stejnegeri	0100101010020 0 0 1 0 0	10110001001? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
M. carlhubbsi	0100101010020 0 0 1 0 0	10110001011? 1 1 0 0 0	021 3 0000000 ?	0 1	10001010
P. gangetica	0100100100??0 0 0 1 (01) 0	0?0101010?1 0 1 0 0 0	00? ? 0001100 ?	0 0	01000100
I. geoffrensis	0100100101?1 1 0 1 (01) 0	0?0100010?1 0 0 1 0 0	00? ? 1010011 1	0 1	00001100
P. blainvillei	0000000101?1 1 1 1 0 0	0?1110011101? 1 0 1 0 1	00? ? 1010001 0	0 0	01001100
L. vexillifer	0100000101?0 0 0 1 0 0	0?0100011101?(01) 0 1 0 0 0	00? ? 1000001 1	0 1	01101100
M. monoceros	1100000000?0 (01) (01) 1 0 0	0?0100110?1 0 1 0 0 0	00? ? 0000001 0	1 1	00011011
D. leucas	1100000000?0 (01) (01) 1 0 0	0?0100110?1 0 1 0 0 0	00? ? 0000001 0	1 (01)	00011011
P. phocoena	0100000001?1 1 0 1 1 0	0?0100110?1 0 1 0 0 0	10? ? 1000001 1	1 (01)	01011110
P. spinipinnis	0100000001?1 1 1 1 1 0	0?0100110?1 0 1 0 0 0	10? ? 1000001 1	1 1	01011110
P. sinus	0100000001?1 1 0 1 1 0	0?0100110?1 0 1 0 0 0	10? ? 1000001 1	1 (01)	01011110
P. dalli	0100000001?1 1 0 1 1 0	0?0100110?1 0 1 0 0 0	10? ? 1000001 (01)	1 (01)	01111110
N. phocaenoides	0100000001?1 1 1 1 0 0	0?0100110?1 1 0 1 0 0	10? ? 1000001 1	1 1	01011110
O. brevirostris	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	1 1	01011111
P. electra	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
F. attenuata	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01001111
P. crassidens	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 (01)	0 1	00001111
O. orca	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
G. melaena	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
G. macrorhynchus	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. bredanensis	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. fluviatilis	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. chinensis	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. teuszii	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. albirostris	0100000000?0 0 0 1 0 0	0?0100010?1 1 0 (01) 0 0	01? ? 0000001 1	0 (01)	01101111
L. acutus	0100000000?0 0 0 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. obscurus	0100000000?0 0 0 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. obliquidens	0100000000?0 0 0 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. cruciger	0100000000?0 0 0 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. australis	0100000000?0 0 0 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. hosei	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
D. delphis	0100000000?0 0 0 1 0 ?	0?0100110?1 1 0 1 0 0	01? ? 0010001 1	0 1	01101111
T. truncatus	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
G. griseus	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. attenuata	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. frontalis	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. coeruleoalba	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. longirostris	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
S. clymene	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
L. peronii	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 ? 0 0	01? ? 0000001 1	0 ?	011?1111
L. borealis	0100000000?0 0 0 1 0 0	0?0100110?1 1 0 1 0 0	01? ? 0000001 1	0 1	01101111
C. heavisidii	0100000000?0 0 1 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0010001 1	0 1	01101111
C. hectori	0100000000?0 0 1 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0010001 1	0 1	01101111
C. eutropia	0100000000?0 0 1 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0010001 1	0 1	01101111
C. commersonii	0100000000?0 0 1 1 0 0	0?0100010?1 1 0 1 0 0	01? ? 0010001 1	0 1	01101111

	1460	1470	1480	1490	1500	1510	1520
B. taurus	0000?000 0	000000 0	00?0000?0???? ?	??????0?????? ?	??0??0?0000?000?0?00?????10?0??		
C. dromedarius	0000?000 ?	000000 0	00?0000?0???? ?	??????0?????? ?	??0??0?0000?000?0?00?????10?0??		
T. tajacu	0000?000 0	000000 0	00?0000?0???? ?	??????0?????? ?	??0??0?0000?000?0?00?????10?0??		
A. americana	0000?000 0	000000 0	00?0000?0???? ?	??????0?????? ?	??0??0?0000?000?0?00?????10?0??		
T. napu	0000?000 ?	000000 0	00?0000?0???? ?	??????0?????? ?	??0??0?0000?000?0?00?????10?0??		
Archaeocete	0?00??00 ?	000000(02)	00?0?00???010 0	1000000000000 1	00000000???????????????????????		
B. mysticetus	0002??00 ?	001122? ?	???????0???001 0	0???0000000? ?	0?20000?000?000?00010??00070???		
E. glacialis	00020000 0	001122? ?	???????0???001 0	0?0000000000? ?	0120010?100?000?00010??00070???		
B. acutorostrata	00000000 0	001122? ?	???????0???001 0	0?0000000000? ?	0100000?000?00100010??00070???		
B. physalus	00000000 0	001122? ?	???????0???001 0	0?0000000000? ?	0100000000?00100010??00070???		
E. robustus	00000000 0	001122? ?	???????0???001 0	0?0000000000? ?	0???0????00?00120010??00070???		
M. novaeangliae	00000000 0	001122? ?	???????0???001 0	0?0000000000? ?	0?0001??100?00100010??00070???		
P. catodon	11001000 0	010210 0	0000000?0?002 0	0001011010001 0	??100000010?1112101110?10041 0???		
K. breviceps	11?01000 0	000210 0	0000000?0?002 0	0001011110001 0	1020000011?110?1?1110?10150??		
K. simus	11?01000 0	000200 0	0000000?0?002 0	0001011110001 0	1020000001?11121?1110?10150??		
Z. cavirostris	11001000 0	000220 0	1000101002?002 0	2000011010011 0	10?0000001010011?0?110110110111		
B. bairdii	11001000 0	000220 2	1000001002?002 0	2000011010011 0	10?0000001010011?1?110111120111		
H. planifrons	11001000 0	000220 0	1000101002?002 0	2000011010011 0	?020000001010011?0?110110110111		
T. shepherdi	11001000 0	000110 0	1000001002?002 0	2000011010011 0	?0?0000001010011?1?110110110111		
M. densirostris	11001000 0	000220 2	1000121202?002 0	2000011010011 0	?0?0000001010011?0?111110110111		
M. bidens	11001000 0	000220 2	1000111113002 0	2000011010011 0	?0?0000001010011?0?110110110111		
M. europaeus	11001000 0	000220 2	1000101111002 0	2000011010011 0	10?0000001010011?0?110110110111		
M. peruvianus	11001000 ?	000220 2	1000?0120?0?? 0	2000011010011 0	??????????10?00112??11???????????		
M. mirus	11001000 0	000220 2	1000?1?010002 0	200?011010??1 0	?0?0000001010011?0?110110110111		
M. layardii	11001000 0	000220 2	1000111114002 0	200?011010??1 0	?0?0000001010011?0?110110110111		
M. grayi	11001000 0	000220 2	1000101111002 0	200?011010??1 0	10?0000001010011?0?110110110111		
M. hectori	11001000 0	000220 2	10001?1010002 0	200?011010??1 0	?0?0000001010011?0?110110110111		
M. ginkgodens	11001000 0	000220 2	1000101111002 0	2000011010011 0	?0?0000001010011?0?110110110111		
M. stejnegeri	11001000 0	000220 2	1000111213002 0	2000011010011 0	?0?0000001010011?0?110110110111		
M. carlhubbsi	11001000 0	000220 2	1000101112002 0	200?011010??1 0	10?0000001010011?0?110110110111		
P. gangetica	11001011 1	110110 0	0001000?0?011 1	2100110011110 1	0?000117?10?000?2??110111160101		
I. geoffrensis	11011010 1	110112 0	0010000?0?111(01)	2110111010000(01)	0101200021?000?21?110110110100		
P. blainvillei	11101000 1	110110 0	0100000?0?113 0	2110111110000 0	0101100?21?000?21?110110110100		
L. vexillifer	11111000 1	110111 0	0000000?0?111 1	2110111010110 1	0001000021?000?21?110111130100		
M. monoceros	11101000(01)	100220 0	0000100?0?111 0	0110111010000 0	0000100??10?000?21?110111110100		
D. leucas	11101000 1	100000 0	0000000?0?111 0	0110111010000 0	0101100011?000?21?110111110101		
P. phocoena	11101110 1	100110 1	0000000?0?113 0	1110111010000 0	0130100101?000?21?110011110100		
P. spinipinnis	11101110 1	100110 1	0000000?0?113 0	1110111010000 0	0130100101?000?21?110111110100		
P. sinus	11101110 1	100110 1	0000000?0?113 0	1110111010000 0	0130100101?000?21?110011110100		
P. dalli	11101110(01)	100110 0	0000000?0?113 0	1110111010000 0	0130100101?000?21?110111110100		
N. phocaenoides	11101110 1	100110 1	0000000?0?113 0	1110111010000 0	?130100111?000?21?110111110100		
O. brevirostris	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0030100011?000?21?110111110100		
P. electra	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
F. attenuata	11101000 1	100000 0	0000000?0?111 0	0110111010000 0	0030100101?000?21?110111110100		
P. crassidens	11101000 1	100000 0	0000000?0?111 0	011?111010020 0	0130100101?000?21?110111110100		
O. orca	11101000 1	100000 0	0000000?0?111 0	0110111010000 0	?130100011?000?21?110111110100		
G. melaena	11101000(01)	100000 0	0000000?0?111(01)	0110111010000 0	0030100101?000?21?110001110100		
G. macrorhynchus	11101000(01)	100000 0	0000000?0?111(01)	0110111010000 0	0030100101?000?21?110001110100		
S. bredanensis	11101000 1	100111 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. fluviatilis	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. chinensis	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. teuszii	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. albirostris	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. acutus	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. obscurus	11101000 1	100110 0	0000000?0?111 0	011?111010020 0	0130100101?000?21?110111110100		
L. obliquidens	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. cruciger	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. australis	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. hosei	11101000 1	100110 0	0000000?0?111 0	011?111010020 0	0130100101?000?21?110111110100		
D. delphis	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
T. truncatus	11101000 1	100110 0	0000000?0?111(01)	0110111010000 0	0130100101?000?21?110111110100		
G. griseus	11101000(01)	100000 0	1000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. attenuata	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. frontalis	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. coeruleoalba	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. longirostris	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
S. clymene	11101000(01)	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
L. peronii	11101000 1	100110 0	0000000?0?111 0	011?111010020 0	?130100101?000?21?110111110100		
L. borealis	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110111110100		
C. heavisidii	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110011110100		
C. hectori	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110011110100		
C. eutropia	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110011110100		
C. commersonii	11101000 1	100110 0	0000000?0?111 0	0110111010000 0	0130100101?000?21?110011110100		

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[                1530        1540        1550        1560                1570        1580        1590        16001604]
[                .           .           .           .                   .           .           .           .       ]
                                                                                                morphological data end>  ]
B. taurus        ?0?00?0?0???0????????00??00?0?00? 0  0000001 0  00?001000000000000000000000000000000
C. dromedarius   ?0?00?0?0???0????????00??00?0?00? 0  0000001 0  00?001000000000000000000000000000000
T. tajacu        ?0?00?0?0???0????????00??00?0?00? 0  0000001 0  00?001000000000000000000000000000000
A. americana     ?0?00?0?0???0????????00??00?0?00? 0  0000000 0  00?001000000000000000000000000000000
T. napu          ?0?00?0?0???0????????00??00?0?00? ?  0000001 0  00?001000000000000000000000000000000
Archaeocete      ?????????????????????????????????? ?  ?000000 0  00???000?????00010?0????11000????11
B. mysticetus    ?0?00?0?0???0????????0???00?0?00? 1  0111120 0  1?10?011000111111111111111111111112
E. glacialis     ?0?00?0?0???0????????????00?0?00? 1  0111021(01)111010110001111111111111111111112
B. acutorostrata ?0?00?0?0???0????????????00?0?00? 1  1111100 0  00001111000111111111111111111111112
B. physalus      ?0?00?0?0???0????????????00?0?00? 1  1111100 0  00001111000111111111111111111111112
E. robustus      ?0?00?0?0???0????????????00?0?00? 1  2111012 ?  00001011000111111111111111111111112
M. novaeangliae  ?0?00?0?0???0????????????00?0?00? 1  1111100 0  00001111000111111111111111111111112
P. catodon       ?1010?0?0???0????????00?000?000?? 0  2000000 0  00?100001111111111111111111111111112
K. breviceps     ?1010?0?0???0????????00?000?000?? 2  1000000 0  00?100001111111111111111111111111112
K. simus         ?1010?0?0???0????????00?000?000?? 2  1000000 0  00?100001111111111111111111111111112
Z. cavirostris   01101000101?0???????110000011010 2  1000000 0  00?100001111111111111111111111111112
B. bairdii       01101100101?0???????110000011010 1  1000000 0  00?100001111111111111111111111111112
H. planifrons    01101100101?0???????110000011010(01)1000000 0  00?100001111111111111111111111111112
T. shepherdi     01101000101?0???????110000011010 2  1000000 0  00?100001111111111111111111111111112
M. densirostris  11101000101?0???????110000111011 2  1000000 0  00?100001111111111111111111111111112
M. bidens        11101010101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. europaeus     11101?0?101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. peruvianus    ?????????????????????????????????? ?  1000000 0  00?100?0???111111111111111111111112
M. mirus         11101?0?101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. layardii      11101?0?101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. grayi         11101?0?101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. hectori       11101?0?101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. ginkgodens    11101?0?101?0???????110000111010 ?  1000000 0  00?100001111111111111111111111111112
M. stejnegeri    11101010101?0???????110000111011 ?  1000000 0  00?100001111111111111111111111111112
M. carlhubbsi    11101010101?0???????110000101110 ?  1000000 0  00?100001111111111111111111111111112
P. gangetica     01101110101?0???????0100??000??? 1  2000000 0  00?100001111111111111111111111111112
I. geoffrensis   0110110?10?110?10011100???000?? 0  2000000 0  00?100001111111111111111111111111112
P. blainvillei   0110110?10?110?10011100???000?? 1  1000000 0  00?100001111111111111111111111111112
L. vexillifer    01101110101?110?10010100???000?? 1  1000000 0  00?100001111111111111111111111111112
M. monoceros     0110111010?110?0001111111?00010 0  0000000 0  00?100001111111111111111111111111112
D. leucas        01101110101?1101000111111?00010 0  2000000 0  00?100001111111111111111111111111112
P. phocoena      0110111110?111101111111001?10010 ?  1000000 0  00?100001111111111111111111111111112
P. spinipinnis   0110111110?1111?1111111001?10010 ?  1000000 0  00?100001111111111111111111111111112
P. sinus         01101111110?111101111111001?10010 ?  1000000 0  00?100001111111111111111111111111112
P. dalli         0110111110?111101111111001?10010 0  1000000 0  00?100001111111111111111111111111112
N. phocaenoides  0110111110?111101111111001?10010 0  0000000 0  00?100101111111111111111111111111112
O. brevirostris  01100?1010?1100001111001?10010 2  1000000 0  00?100001111111111111111111111111112
P. electra       01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
F. attenuata     01100?1010?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
P. crassidens    01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
O. orca          01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
G. melaena       01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
G. macrorhynchus 01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. bredanensis   01100?1010?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
S. fluviatilis   01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. chinensis     01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. teuszii       01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. albirostris   01100?1011?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
L. acutus        01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. obscurus      01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. obliquidens   01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. cruciger      01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. australis     01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. hosei         01100?1011?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
D. delphis       01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
T. truncatus     01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
G. griseus       01100?1010?1100001111001?10010 2  1000000 0  00?100001111111111111111111111111112
S. attenuata     01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. frontalis     01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. coeruleoalba  01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. longirostris  01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
S. clymene       01100?1010?1100001111001?10010 0  1000000 0  00?100001111111111111111111111111112
L. peronii       01100?1010?1100001111001?10010 1  0000000 0  00?100001111111111111111111111111112
L. borealis      01100?1010?1100001111001?10010 0  0000000 0  00?100001111111111111111111111111112
C. heavisidii    01100?1010?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
C. hectori       01100?1010?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
C. eutropia      01100?1010?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
C. commersonii   01100?1010?1100001111001?10010 ?  1000000 0  00?100001111111111111111111111111112
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