Radiation of Extant Cetaceans Driven by Restructuring of the Oceans

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Abstract.—The remarkable fossil record of whales and dolphins (Cetacea) has made them an exemplar of macroevolution. Although their overall adaptive transition from terrestrial to fully aquatic organisms is well known, this is not true for the radiation of modern whales. Here, we explore the diversification of extant cetaceans by constructing a robust molecular phylogeny that includes 87 of 89 extant species. The phylogeny and divergence times are derived from nuclear and mitochondrial markers, calibrated with fossils. We find that the toothed whales are monophyletic, suggesting that echolocation evolved only once early in that lineage some 36–34 Ma. The rorqual family (Balaenopteridae) is restored and mitochondrial markers, calibrated with fossils. We find that the toothed whales are monophyletic, suggesting that echolocation evolved only once early in that lineage some 36–34 Ma. The rorqual family (Balaenopteridae) is restored and mitochondrial markers, calibrated with fossils. 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Two hypotheses regarding cetacean evolution relate to the roles of biological and physical drivers. One hypothesis holds that modern cetacean diversity is in part attributable to a rapid adaptive radiation following a transition into an open adaptive zone (sensu Simpson 1953), which occurred early in the history of crown Cetacea as the 2 sister clades, the toothed and baleen whales, acquired their respective echolocation and filter-feeding abilities. Such transitions into unoccupied regions of ecological niche space are frequently associated with rapid phenotypic change—often leading to increased structural disparity—and with species diversification, owing to a relaxation of ecological constraints and exploitation of unsaturated ecological niche space during the early phase of the radiations (Schluter 2000; Rabosky and Lovette 2008a). Such ecological opportunities arise when resources are abundant with few competitor lineages present and they are widely believed to trigger the explosive diversification involved in species-level radiations (Weir 2006; Phillimore and Price 2008). Previous studies indicate that both toothed and baleen whales showed a rapid increase in ecological and morphological disparity in the early Oligocene (Fordyce 2003), as well as rapid speciation early in the evolution of extant taxa (Nikaido et al. 2001), consistent with the adaptive-radiation hypothesis.

A second hypothesis holds that speciation since late Eocene times was determined by the tectonically-driven rearrangement of physical barriers, features of the thermohaline circulation, and water temperature, all of which interact today to define cetacean habitat and food distribution (e.g., Pastene et al. 2007). Cenozoic ocean history is characterized by numerous changes in physical geography, circulation, sea level, and climate, with 2 intervals noteworthy for major events that could have influenced cetacean diversification. First, the tectonic opening of the Drake Passage between South America and Antarctica, and of the Australian–Antarctic Tasman seaway, created the Southern Ocean with a free-flowing Antarctic Circumpolar Current (Scher and Martin 2006; Livermore et al. 2007; Fig. 1). This event was coincident with the late Eocene to early Oligocene climatic change from greenhouse to icehouse world (Coxall and Pearson 2008; Lear et al. 2008). Atmospheric CO2 levels decreased, and Antarctic ice sheets of the Oi-1 glaciation expanded rapidly, associated with changes in calcite compensation depth, Southern Ocean upwelling, and increasing primary productivity (Coxall et al. 2005; Scher and Martin 2006; Livermore et al. 2007; Lear et al. 2008). Second, a cascade of tectonic, paleoceanic, and climatic changes occurred during the late Miocene to early Pliocene. Global warmth was followed by Antarctic ice growth at the middle Miocene climate transition ~14 Ma (Shevenell et al. 2008), and since the late Miocene there has been a general cooling and/or ice growth trend (positive δ18O shift) and increased productivity (negative δ13C shift) (Zachos et al. 2001). Significant changes occurred with the closure of the eastern Tethys link between the Mediterranean and Indian oceans ~13–10 Ma (Harzhauser and Piller 2007), restriction of the deep

Indo-Pacific seaway ~12–5 Ma (Kuhnt et al. 2004), and restriction then closure of the Central American seaway ~14–4.2 Ma (Jain and Collins 2007; Fig. 1). Cooling and geographic changes affected thermohaline circulation (Thomas and Via 2007), including North Atlantic deep water circulation following the closure of the Central American seaway (Lear et al. 2003). Enhanced biogenic phosphatic sedimentation has been linked to upwelling (Diester-Haass et al. 2005) and to a marked negative δ13C shift reflecting enhanced global marine productivity about 7.6–6.3 Ma (Zachos et al. 2001).

Here, we elucidate the evolution of extant cetaceans by constructing a molecular phylogenetic tree containing almost all the extant cetacean species. Our multipartitioned data set includes a sequence alignment of 15 mitochondrial and nuclear genes and incorporates multiple fossil calibration points in a relaxed clock framework. By reading the signatures of species diversification processes in the time-calibrated molecular phylogeny, we can test hypotheses concerning the radiation of recent Cetacea. We assess the role of adaptation in driving cladogenesis early in the evolution of extant whales as well as the effects of large-scale ocean-restructuring events on cetacean diversification.

**METHODS**

Nucleotide sequences of 6 mitochondrial and 9 nuclear genes were obtained from GenBank for 87 of 89 extant cetacean species and 3 outgroup taxa (Hippopotamus amphibius, Sus scrofa, and Bos taurus). Sequences were manually aligned to form a data set of 16,175 characters (6,666 mitochondrial and 9,509 nuclear). GenBank accession numbers are listed in Appendix S1 (available from http://www.sysbio.oxfordjournals.org/). The data supermatrix (matrix combining several types of data, in this case different gene sequences, available from various groups of included taxa) is available at TreeBase, accession number S2467. Taxonomic and vernacular names follow Rice (1998) unless specified (see Table 1). The sequence alignment was partitioned so that separate substitution models could be applied to different parts of the data set. The 2 mitochondrial ribosomal RNA genes, 12S and 16S, were concatenated to form a single partition. All noncoding sequences (actin intron, alb intron, and sry flanking regions) were combined into a single data partition. The 13 protein-coding genes were partitioned by gene and were further divided into first + second versus third codon sites following Shapiro et al. (2006). Estimation of the phylogeny and divergence times was performed in 2 steps. First, Bayesian phylogenetic inference was conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), with each data partition being assigned a separate substitution model, selected using Bayesian information criterion scores determined by Modelgenerator (Keane et al. 2006). Posterior probability distributions of parameters, including the tree topology, were approximated using Markov chain Monte Carlo simulation. One cold and 3 heated Markov chains were run for 90,000,000 steps.
Following a discarded burn-in of 30,000,000 steps, samples from the Markov chain were taken every 1000 steps. Parameters were checked for acceptable mixing and convergence to the stationary distribution with the program Tracer 1.4 (Rambaut and Drummond 2007). The posterior sample of trees was analyzed using the diagnostic software AWTY (Nylander et al. 2008), and convergence of topological split frequencies was found to be satisfactory. A maximum clade-credibility tree was obtained from the set of trees sampled from the posterior.

Second, divergence time estimation was carried out using a relaxed molecular clock approach, as implemented in r8s 1.7 (Sanderson 2002). Date estimates were
Table 1. Formal and vernacular names of cetacean taxa with representative species and included families where applicable (follows Rice 1998; Fordyce and Muizon 2001)

| Formal name       | Vernacular names                               | Representative species                  | Included families |
|-------------------|------------------------------------------------|----------------------------------------|-------------------|
| Balaenidae        | Right whales, balaenids                         | *Balaena mysticetus*, bowhead whale    |                   |
| Neobalaenidae     | Pygmy right whale                               | *Caperea marginata*, pygmy right whale, only |
| Balaenopteridae   | Rorquals, balaenopterids                        | *Balaenoptera acutorostrata*, minke whale |                   |
| Eschrichtiidae    | Gray whale                                      | *Eschrichtius robustus*, gray whale, only |                   |
| Physeteroidea     | Sperm whales                                    | *Physaster macrocephalus*, sperm whale | *Physasteridae*, *Kogiidae* |
| Physetidae        | [Giant] sperm whale                             |                                        |                   |
| Kogiidae          | Pygmy sperm whales                              | *Kogia breviceps*, pygmy sperm whale |                   |
| Platanistidae     | Ganges and Indus River dolphins                 | *Platanista gangetica*, Ganges river dolphin |                   |
| Ziphidae          | Beaked whales, ziphiiids                        | *Ziphius cavirostris*, Cuvier’s beaked whale |                   |
| Delphinida        | Lipotidae, Iniidae, Pontoporiidae, Phocoenidae, Monodontidae, Delphinidae | Lipotidae, Iniidae, Pontoporiidae |                   |
| Delphinida        | Lipotidae                                       | *Lipotes vexillifer*, baiji |                   |
| Delphinida        | Iniidae                                         | *Inia geoffrensis*, boto |                   |
| Delphinida        | Delphinidae                                     | *Pontoporia blainvillei* |                   |
| Delphinida        | Phocoenidae                                     | *Phocoena phocoena*, harbor |                   |
| Delphinida        | Monodontidae                                    | *Monodon monoceros*, narwhale |                   |
| Delphinida        | Delphinidae                                     | *Delphinus delphis*, common dolphin |                   |

Table 2. Fossils used for calibration of the molecular clock analysis

| Group name                      | Minimum constraint | Maximum constraint | Defining taxon                      | Age (Ma) |
|---------------------------------|--------------------|--------------------|-------------------------------------|----------|
| Cetacea versus outgroup         | 53.6               | 56                 | *Himalayacetus subbathuensis*        | 53.5     |
| Crown group Cetacea             | 35.0               |                    | *Lamnacetus denticrenatus*           | 34.2     |
| Crown group Mysticeti           | 28.0               |                    | Un-named archaic right whale         | 28       |
| Crown group Balaenopteridae     | 7.3                |                    | “Megaptera” miocaena                 | 8.2–7.3  |
| Inioidae–Delphinoidea           | 23.5               |                    | *Keniromon ?sp.*                     | 23.5     |
| Crown group Inioidea            | 12.0               |                    | *Brachydolphus mazzesi*              | 15–12    |
| Crown group Delphinoidea        | 10.0               |                    | *Salumiphocaena stocktoni*           | 11–10    |
ring anywhere in the tree; accordingly, we repeated our analysis after excluding the most recent 10 Ma of evolutionary history to control for the possibility that recent changes in diversification rates obscured our ability to detect a rapid diversification during the early phase of the radiation. We used a likelihood approach based on the birth–death process to contrast the fit of density-dependent and constant-rate models of diversification (Rabosky and Lovette 2008a).

To test for shifts in diversification rates during the putative episodes of abiotic forcing (35–31 Ma; 13–4 Ma), we implemented an extension of the discrete-shift method used in several previous studies (Barraclough and Vogler 2002; Rabosky 2006b). We computed the likelihoods of the phylogenetic data under models with constant speciation (pure birth) or constant speciation/extinction (birth–death) and compared these with the likelihood under models in which the speciation rate during the restructuring period was treated as a free parameter. Significance was assessed using a likelihood-ratio test. Additional details can be found in Rabosky (2006b). All analyses were conducted using extensions of the LASER package for the R programming/statistical environment (Rabosky 2006a). We did not include extinction in the final model because 1) estimates under a constant rate birth–death model tended toward 0 and 2) it is difficult to obtain meaningful estimates of separate extinction and speciation parameters under discrete-shift models similar to those considered here because confidence intervals on extinction rates are very large.

We also conducted a profile likelihood analysis to investigate the likelihood of diversification-rate shifts through time. We assumed a model whereby a baseline speciation rate $\lambda_1$ shifts to a new rate $\lambda_2$ during a temporal window with a fixed width of 6 Ma; a window centered at $x = 20$ Ma would thus define a model with speciation rate $\lambda_1$ on the interval $35–23$ and $17–0$ Ma and rate $\lambda_2$ on $23–17$ Ma. We computed the likelihood of this model across 2500 equally spaced points between 33 and 2 Ma and plotted both the estimated rates and the model likelihood to visualize time intervals with exceptionally high (or low) diversification rates.

**RESULTS AND DISCUSSION**

**Cetacean Phylogeny and Speciation**

Our phylogenetic analysis strongly supports the mutual monophyly of the 2 extant (crown) clades, Mysticeti (baleen whales) and Odontoceti (toothed whales and dolphins), with a posterior probability of 1.00 (Fig. 2). This fundamental division among the living Cetacea has been recognized since the mid-nineteenth century. Under a relaxed clock model, the timing of the Mysticeti–Odontoceti divergence is estimated at 36 Ma (Fig. 3). Significantly, these results, from a larger data set than previous studies, are consistent with most previous estimates of the phylogeny and divergence times.

Some molecular studies have radically proposed a paraphyletic origin of odontocetes. For example, Milinkovitch et al. (1993) argued that the sperm whale (Physeteridae) plus the pygmy sperm whales (Kogiidae) are more closely related to mysticetes than to other odontocetes. Verma et al. (2004) suggested that the Ganges/Indus River dolphins *Platanista* are more closely related to mysticetes than to any other odontocete. These evolutionary scenarios would imply that echolocation in odontocetes evolved twice, or alternatively evolved once in archaeocetes, to become secondarily lost in early mysticetes, as proposed by Milinkovitch (1997). Such changes would suggest either parallel evolution or complete loss of point-by-point similarities in the complex acoustic apparatus. However, echolocation is ubiquitous among living odontocetes and is thus predicted to have been present in the most recent common ancestor of the crown-group species. The presence of echolocation has been inferred for the oldest described fossil odontocete, *Simocetus rayi* dated at $\sim 32$ Ma (Fordyce 2002b). Living mysticetes are not known to echolocate in the manner of odontocetes, and extinct baleen whales lack skull features such as the expanded facial fossa and ascending process of maxilla which, in odontocetes, are linked to echolocation (Cranford 2000).

We suggest that echolocation evolved with the origin of the crown Odontoceti about 36–34 Ma and agree with other molecular and morphological studies that have rejected the hypothesis of paraphyly for odontocetes (Heyning 1997; Messenger and McGuire 1998; Gatesy et al. 2002; Geisler and Sanders 2003; Price et al. 2005).

The estimated origin of Neoceti at around 36 Ma concurs with several previous estimates (Nikaido et al. 2001; Sasaki et al. 2005). The date is close to the minimum age constraint set for the split, which is based on the oldest fossil member of Neoceti, the archaic mysticete *Llanocetus denticrenatus* (Table 2). A 36 Ma origin, however, contrasts dramatically with the early Eocene split around 50 Ma proposed by Cassens et al. (2000) on the basis of a single delphinid calibration. There is no fossil evidence to support such an early origin of the neocete groups, whereas strong support exists for a late Eocene split. An origin of Neoceti around 50 Ma (Cassens et al. 2000) implies a long ghost lineage of stem Neoceti spanning 14 Ma, a time interval that has yielded a well-sampled and phylogenetically well-analyzed sequence of archaeocetes (e.g., Thewissen 1998; Gingerich 2005).

The data also corroborate fossil evidence that among the toothed whales, 4 high-level clades were established about 30 Ma: sperm whales (Physeteroidea); the highly disparate *Platanista* river dolphins (Platanistidae); the deep-diving, suction-feeding beaked whales (Ziphiidae); and the Delphinida—dolphins of family Delphinidae and relatives (Fig. 3). A position of the Ganges/Indus river dolphins (*Platanista*) more basal than the beaked whales is controversial (Muizon 1988; Heyning 1997; Arnason et al. 2004; May-Collado and Aagnarsson 2006; Aagnarsson and May-Collado 2008) but supports a previous phylogenetic analysis based on short interspersed nuclear elements (SINEs) (Nikaido et al. 2001). The recent ziphiid lineage diversified...
gradually 20–10 Ma, with a more rapid speciation since 9–10 Ma. For the Delphinida, our results show little diversification before 11 Ma but porpoises (Phocoenidae) and especially delphinids (Delphinidae) subsequently speciated dramatically. As a result of a rapid radiation since 11 Ma, the delphinid clade is now the most speciose living group of Cetacea (Rice 1998) (35 of 89 known species: discussed below), and the most ecologically versatile, occupying tropical to polar latitudes, neritic and oceanic waters, estuaries, and sometimes rivers.

The filter-feeding baleen whales also show deep, early (29–26 Ma) divergences for the right whale (Balaenidae),
FIGURE 3. (Continued)
pygmy right whale (Neobalaenidae), and the gray whale and rorqual clade. Our analyses suggest that baleen-assisted filter-feeding evolved sometime between the origin of the Mysticeti about 35 Ma and the divergence of recent lineages by 28 Ma. The topology of our mysticete phylogeny is consistent with recent studies on SINEs and complete mitochondrial data (Sasaki et al. 2005; Nikaido et al. 2006). Contrary to most other molecular studies (Arnason and Gullberg 1994; Rychel et al. 2004; Agnarsson and May-Collado 2008), we find strong evidence (posterior probability of 1.00) that the gray whale, which is a benthic feeder, is phylogenetically distinct from the gulp-feeding rorquals. Our findings thus support morphological studies (Deméré et al., 2005; Bisconti, 2007; Steeman, 2007; Deméré et al., 2008) and indicate that the evolution of gulp feeding and the specialized structures related to this feeding technique was a single event unique to the rorqual lineage (see Appendix S3). Among extant baleen whales, only the rorquals show substantial modern diversity. We estimate that the major rorqual lineages evolved 18–10 Ma, whereas evidence for this radiation is equivocal in the fossil record prior to ca. 10 Ma (Deméré et al. 2005). Further discussion of the phylogeny and fossil range of family-level lineages is provided in Appendix S3.

Testing Hypotheses on Evolutionary Drivers

We investigated 2 general hypotheses for large-scale patterns in the diversification of modern cetaceans: 1) that extant cetacean diversity was driven by rapid changes into an open adaptive zone like the initial radiation in stem Cetacea (the adaptive radiation hypothesis) (Nikaido et al. 2001) and 2) that abiotic drivers, including physical restructuring of the oceans, played a major role in the radiation of extant cetaceans (the abiotic hypothesis) (Fordyce 1980, 2003).

We predicted that if extant cetacean lineages experienced early adaptive radiation, then they should show an early burst of diversification, followed by a subsequent slowdown in rates through time. We tested this hypothesis (Nee et al. 1992; Rabosky and Lovette 2008a) by computing the γ statistic for our time-calibrated phylogeny of extant whales. We found no evidence for a temporal slowdown in the rate of speciation for the complete cetacean phylogeny or for the 2 major cetacean suborders, and our results are virtually identical for the complete tree and for the suborders considered separately (Table 3). This suggests that diversification rates in extant lineages have not decreased through time.

Although high background extinction rates could obscure the signal (Rabosky and Lovette 2008b), likelihood analyses using constant diversification models with and without extinction provide no evidence in favor of a model that includes extinction (Table 4). Furthermore, there is no evidence for density dependence of diversification rates through time (Table 4), as predicted under adaptive radiation models (Nee et al. 1992; Rabosky and Lovette 2008a). In combination, these results do not support a scenario in which early crown cetacean diversification was driven by ecological opportunity. It is possible that diversification patterns consistent with the adaptive-radiation model occurred primarily among lineages (noted below) that subsequently went extinct, as for major mammalian clades during the Paleocene (Bininda-Emonds et al. 2007). If this is so, the process has not left a signature in the distribution of speciation times of extant cetacean lineages.

We then investigated the abiotic hypothesis of cetacean diversification by testing for associations between lineage-diversification rates and geologically established paleoceanic changes. To test whether ocean restructuring was associated with increased diversification rates, we compared the likelihood of the cetacean phylogeny under 2 models: constant-rate diversification and time-varying diversification rate (Rabosky 2006b). Specifically, we predicted that a baseline speciation rate λ1 would shift to a new rate λ2 during putative ocean-restructuring periods of 35–31 and 13–4 Ma. We found a significantly better fit for the time-varying model (“ocean restructuring” in Table 5) over the 2 constant-rate null models (“pure birth” and “birth–death” in Table 5) (likelihood ratio test = 5.878, P = 0.015, df = 1; Table 5). Parameters estimated under this model suggest that there was a rise in the speciation rate during these time periods (“background” versus “elevated” rates in Table 5). Separate analysis of each temporal interval (35–31 Ma; 13–4 Ma) supports these results (Table 5). Compared with the 13- to 4-Ma period, however,
TABLE 4. Maximum-likelihood analysis of diversification in cetaceans assuming a lag time for species recognition of 2 Ma (e.g., analysis from Table 3 was repeated, but most recent 2 Ma of phylogeny were excluded)

| Model                        | Parameters | LogL      | AIC       | p     |
|------------------------------|------------|-----------|-----------|-------|
| Pure birth                   | 1          | 14.38     | −26.76    | —     |
| Birth–death                  | 2          | 14.62     | −25.25    | —     |
| Restructure                  | 2          | 16.39     | −28.78    | 0.05  |
| 35–31 Ma only                | 2          | 14.86     | −25.72    | 0.97  |
| 13–4 Ma only                 | 2          | 15.78     | −27.56    | 0.09  |

Notes: The ocean restructuring models provide the best fit to the data. Models and parameters are as described in Table 3.

evidence for elevated rates during the early restructuring period is weak: although it is possible that there might have been some increase in rates during the formation of the Drake Passage at 35–31 Ma, this left only a slight signature in the lineage-accumulation curve for the crown taxa.

A profile analysis of the likelihood of any elevated rate periods during the Cenozoic supports an approximate doubling of the speciation rate between about 9–3 Ma (Fig. 4; see Methods). It is possible that the apparent recent increase in diversification of cetaceans is an artifact of high background extinction rates (Rabosky 2006b), but several lines of evidence argue against this: 1) The comparison of likelihoods, estimated speciation rate, and lineages-through-time plot all show that the high-rate period ends approximately 4–3 Ma rather than showing a continuous increase through to the present as would be expected if the pattern were an artifact of extinction and 2) likelihood analysis of the lineage-accumulation curve (Fig. 5) provides no evidence in favor of a model with extinction (e.g., birth–death) over a model without extinction (e.g., pure birth) (Table 5). It is, however, possible that there is a “lag time” for the recognition of incipient species, which might contribute to an artifactual drop in diversification during the most recent 3 Ma. We find no evidence to suggest that such a lag effect could persist for several million years; many species pairs show divergence times since 1.5 Ma (Fig. 3) and the fossil record suggests cetacean species durations of 1–2 Ma (Fordyce and Muizon 2001). Nonetheless, we conducted a simple analysis to control for this possibility by repeating our analyses after eliminating the most recent 2 Ma from the whale phylogeny, which effectively assumes that there is a lag of up to 2 Ma before incipient species can be recognized as such. Even with this assumption, the ocean-restructuring model fits the data better than the constant-rate diversification models (Table 5).

The fossil record of crown Cetacea also shows a marked increase in the number of extinct genera at 12.5 Ma (Fig. 5). This suggests that a rapid diversification in extinct lineages occurred in the period of paleoceanic restructuring as well. There are, however, several biases connected to the fossil data set (Uhen and Pyenson 2007). Noticeably, the most recent records are probably overrepresented because of better preservation opportunity, sediment availability, and increased taxonomic recognition (Uhen and Pyenson 2007). Also, the drop in numbers of genera at 32.5 Ma is likely due to a scarcity of early Oligocene marine sediments (Fordyce 1980; Uhen and Pyenson 2007).

Cetacean Radiation Pattern and the Abiotic Hypothesis

From the age of the earliest crown cetacean fossil (the mysticete *Llanocetus*, 34.2 Ma), we know that the baleen and toothed whales diverged during the later Eocene cooling shortly before the Eocene/Oligocene boundary (Fig. 3). Our analysis thus seems to support the previously suggested hypothesis (Fordyce 1980) that the opening of the Drake Passage and the initiation of the Antarctic Circumpolar Current spurred the early

TABLE 5. Maximum likelihood analysis of diversification rates in the complete cetacean phylogeny

| Model                        | Parameters | LogL      | AIC       | p     | Background<sup>b</sup> | Elevated<sup>c</sup> |
|------------------------------|------------|-----------|-----------|-------|-------------------------|----------------------|
| Pure birth                   | 1          | 22.53     | −43.05    | —     | 0.1                     | —                    |
| Birth–death (constant rate)  | 2          | 22.53     | −41.05    | —     | 0.1                     | —                    |
| Density dependent, lineard<sup>d</sup> | 2          | 22.53     | −41.04    | 0.990 | —                       | —                    |
| Density dependent, exponential<sup>e</sup> | 2          | 22.59     | −41.18    | 0.740 | —                       | —                    |
| Ocean restructuring<sup>f</sup> | 2          | 25.47     | −46.93    | 0.02  | 0.09                    | 0.14                 |
| 35–31 Ma only<sup>g</sup>    | 2          | 23.11     | −42.23    | 0.28  | 0.1                     | 0.21                 |
| 13–4 Ma only<sup>b</sup>     | 2          | 24.75     | −45.50    | 0.04  | 0.09                    | 0.13                 |

Notes: Pure birth and birth–death models assume constant diversification through time; all other models assume time-varying diversification rates. There is no evidence for density-dependent decline in diversification through time, and the ocean restructuring model has the best overall fit.

<sup>a</sup>Value from likelihood ratio test that the hypothesis model fits the data better than the best-fit constant rate model (pure birth or birth–death).

<sup>b</sup>Estimated background net diversification rate, in lineages/million years.

<sup>c</sup>Estimated net diversification on the hypothesized “high rate” intervals.

<sup>d</sup>Assumes density-dependent exponential decline in speciation rate through time, such that the Speciation rate $\lambda(t) = \lambda_0 e^{-x t}$, where $\lambda_0$ is the initial speciation rate, $N_t$ is the number of lineages alive at time $t$, and $x$ is a rate decrease parameter. Details are given in Rabosky and Lovette (2008).

<sup>e</sup>Assumes density-dependent linear decline in the speciation rate through time, such that the speciation rate is modeled as $\lambda(t) = \lambda_0 (1 - N_t / K)$, where $K$ is a parameter analogous to the carrying capacity in a logistic population growth model.

<sup>f</sup>The ocean restructuring model assumes 2 net diversification rates: one on the proposed ocean restructuring intervals of 35–31 and 13–4 Ma and a second rate at all other times.

<sup>g</sup>One net diversification rate on 35–31 Ma and another at all other times.
radiation of toothed whales, 34–31 Ma. No concurrent molecular deep divergences are apparent among the extant baleen whale lineages, but their fossil record (Fordyce 1980; Deméré et al. 2008) is consistent with the hypothesis that baleen-assisted filter feeding evolved concurrent with the development of the Antarctic Circumpolar Current and, plausibly, silicate upwelling (Berger 2007).

There are few branching events on the molecular tree in the late Oligocene to middle Miocene (Fig. 3). The early middle Miocene was warm (Zachos et al. 2001), and the oceans were linked globally by major low-latitude ocean gateways (Tethys, Indonesian, and Central American seaways) (Fig. 1). Archaic clades of cetaceans that are now extinct and beyond the reach of molecular analysis were diverse and ecologically significant in Oligocene and earlier Miocene times (Fordyce and Muizon 2001). Extinct baleen whale families include toothed clades (Aetiocetidae and Mammalodontidae) and the edentulous, baleen-bearing whales Eomysticetidae, Cetotheriidae sensu stricto, and various stem rorquals. During the Oligocene, several now extinct families of small odontocetes evolved: the long-beaked Eurhinodelphinidae, archaic Platanista relatives (Squalodontidae, Squalodelphinidae, Waipatiidae, and Dalpiazinidae), the stem delphinoid group Kentriodontidae, and Simocetidae (Fordyce 2003). Some of these clades were short ranged, some were Oligocene only, whereas most of the others went extinct in the late middle Miocene to early late Miocene, ∼10–8 Ma (Fordyce and Muizon 2001). This decline coincides with a significant increase (likelihood ratio-based shift statistics: \( P < 0.05 \)) in the diversification rate of Delphinidae (Fig. 3).

The phylogeny reveals an increased speciation rate for delphinids in the second time period (13–4 Ma) during which porpoises and beaked whales also diversify. These radiations occurred as connecting seaways were closed (Tethys, Central American) or restricted (loss of Paratethys, restriction of Indo-Pacific; for significance, see Williams et al. 2002; Kanda et al. 2007), as productivity increased (including the 7.6–6.3 Ma productivity spike) and ocean circulation intensified (Fig. 3). The fossil record also shows an increase in described genera in the late middle to early late Miocene (13.6–7.2 Ma) (Uhen and Pyenson 2007). We attribute the speciation of delphinids to a mix of tectonically-driven vicariant events (above) and to adaptation to geographically-concentrated food sources which perhaps resulted from later Miocene changes in broad patterns of circulation and from intensification of oceanic circulation especially in the Plio-Pleistocene (e.g., Lawrence et al. 2006). Simultaneously, global sea level increased in range, further affecting the water- and gene flow between oceans. Of note are increasingly large sea-level changes since 9 Ma (Miller et al. 2005). The Plioocene was warm initially, but from the middle Pliocene ∼3 Ma (Zachos et al. 2001; Miller et al. 2005), major cooling and enhanced thermohaline ocean circulation led to the establishment of continental northern-hemisphere glaciation. The latter, amplified by orbital cycles, drove the Pleistocene ice age climate including rapid short-term fourth- to sixth-order global sea-level fluctuations of 60–120 m (Fig. 3), which were most intense from the mid-Pleistocene (∼1–0.8 Ma) to the present (Miller et al. 2005). These cyclic sea-level changes would have increased the opportunities for allopatric speciation through phases of basin
isolation caused by sea-level fall. In addition, geologically recent fluctuations in tropical water temperatures, long debated (Cipriano 1997) but only recently established (Lawrence et al. 2006), could explain the evolution of north-south antitropical population pairs and species pairs (Kanda et al. 2007) through allopatric or peripatric speciation.

Compared with delphinids, other extant cetacean groups experienced modestly or minimally accelerated radiation in the second period of ocean restructuring tested in the abiotic hypothesis. Baleen whales show only modest increase in diversity. Most species feed in pelagic high-latitude oceans where the changes following the closure of shallow equatorial gateways were probably not dramatic, particularly in the southern hemisphere. An increase in speciation rate occurred in the beaked whales since 10 Ma. The oceanic feeding grounds of the deep diving, mainly squid-eating beaked whales and sperm whales, may have been less affected compared with ocean delphinid habitats and food resources. For the *Mesoplodon* beaked whales, the stepped phylogeny perhaps reflects successive invasions of increasingly deeper and trophically distinct water masses within the developing global thermohaline circulation. Furthermore, the beaked whale genera *Berardius* and *Hydrodocodon* each contain 2 antitropical (north-south) sister species which arose allopatrically, separated by tropical waters. Although the timing of the invasions into the riverine habitat by various river dolphin lineages is uncertain (Hamilton et al. 2001), this realm was probably not affected by oceanic restructuring either. Interestingly, extant porpoises, which occupy habitats likely to have been affected by oceanic restructuring (Boran et al. 2002), also show a recent relatively rapid diversification. The diversification pattern of cetaceans is thus consistent with the hypothesis that abiotic factors were important in their evolution.

**SUPPLEMENTARY MATERIAL**

Supplementary material can be found at http://www.sysbio.oxfordjournals.org/.

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**REFERENCES**

Agnarsson I, May-Collado L.J. 2008. The phylogeny of Cetartiodactyla: the importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome b to provide reliable species-level phylogenies. Mol. Phylogenet. Evol. 48:964–985.

Ainley D., Ballard G., Ackley S., Blight L.K., Eastman J.T., Emslie S.D., Lesroel A., Olmastro S., Townsend S.E., Tynan C.T., Wilson P., Woehler E. 2007. Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? Antarct. Sci. 19: 283–290.

Arnason U., Gullberg A. 1994. Relationship of baleen whales established by cytochrome b gene sequence comparison. Nature. 367: 726–728.

Arnason U., Gullberg A., Janke A. 2004. Mitogenomic analyses provide new insights into cetacean origin and evolution. Gene. 333: 27–34.

Barraclough T.G., Vogler A.P. 2002. Recent diversification rates in North American tiger beetles estimated from a dated mtDNA phylogenetic tree. Mol. Biol. Evol. 19:1706–1716.

Berger W.H. 2007. Cenozoic cooling, Antarctic nutrient pump, and the evolution of whales. Deep Sea Res. II. 54:2399–2421.

Bierne N., Bonhomme F., David P. 2003. Habitat preference and the marine-speciation paradox. Proc. R. Soc. Lond. Ser. B Biol. Sci. 270: 1399–1406.

Birind-Emonds O.R., Cardillo M., Jones K.E., MacPhee R.D., Beck R.M., Grenyer R., Price S.A., Vois R.A., Gittleman J.L., Purvis A. 2007. The delayed rise of present-day mammals. Nature. 446: 507–512.

Bisconti M. 2007. A new basal balaenopterid whale from the Pliocene of northern Italy. Palaeontology. 50:1103–1122.

Borain J.R., Evans P.G.H., Rosen M.J. 2002. Behavioural ecology of cetaceans. In: Evans P.G.H., Raga J.A., editors. Marine mammals: biology and conservation. New York: Kluwer Academic/Plenum Publishers. p. 197–242.

Cassens I., Vicario S., Waddell VG., Balchowsky H., Van Belle D., Ding W., Fan C., Mohan R.S., Simões-Lopes P.C., Bastida R., Meyer A., Stanhope M.J., Milinkovitch M.C. 2000. Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages. Proc. Natl. Acad. Sci. USA. 97:11343–11347.

Chan K.M., Moore B.R. 2005. SYMME TREE: whole-tree analysis of differential diversification rates. Bioinformatics. 21:1709–1710.

Cipriano F. 1997. Antitropical distributions and speciation in dolphins of the genus *Lagenorhynchus*: a preliminary analysis. Soc. Mar. Mamm. (Spec. Publ.) 3:305–316.

Cowal H.K., Pearson P.N. 2008. The Eocene-Oligocene transition. In: Williams M., Haywood A.M., Gregory F.J., Schmidt D.N., editors. Deep time perspectives on climate change: marking the signal from computer models and biological processes. London (UK): Geological Society London. p. 351–387.

Coxall H.K., Wilson P.A., Palike H., Lear C.H., Backman J. 2005. Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. Nature. 433:53–57.

Cranford T.W. 2000. In search for impulse sound sources in odontocetes. In: Au W.W.L., Popper A.N., Fay R.R., editors. Hearing by whales and dolphins. New York: Springer. p. 109–155.

Deméré T.A., Berta A., McGowen M. 2005. The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. J. Mammal. Evol. 12:99–143.

Deméré T.A., McGowen M.R., Berta A., Gatesy J. 2008. Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete whales. Syst. Biol. 57:15–37.

Dieter-Haass L., Billups K., Emeis K.C. 2005. In search of the late Miocene-early Pliocene “biogenic bloom” in the Atlantic Ocean

**Downloaded from http://sysbio.oxfordjournals.org/ by guest on April 29, 2016**
Lawrence K.T., Liu Z.H., Herbert T.D. 2006. Evolution of the eastern
Fordyce R.E. 1980. Whale evolution and Oligocene southern ocean
Simocetus rayi
Fordyce R.E., de Muizon C. 2001. Evolutionary history of cetaceans: a
Kanda N., Goto M., Kato H., Mcphee M.V., Pastene L.A. 2007. Pop-
Ho S.Y.W., Phillips M.J. 2009. Accounting for calibration uncertainty
Gingerich P.D., ul-Haq M., von Koenigswald W., Sanders W.J., Smith
Geisler J.H., Sanders A.E. 2003. Morphological evidence for the phy-
Gatesy J., Matthee C., DeSalle R., Hayashi C. 2002. Resolution of a
transformation of the basicranium and evolution of hearing in
Geophys. Geosyst. 8:1–11.
Passage and Cenozoic climate: an open and shut case? Geochem.
Lett. 210:425–436.
Cooling and ice growth across the Eocene-Oligocene transition. Earth Planet. Sci.
79–83.
The Indonesian throughflow. In: Cliff P.D., editor. Continent-
336.
Geology. 36:251–254.
May-Collado L., Agnarsson I. 2006. Cytochrome b and Bayesian infer-
Mol. Phylogenet. Evol. 38:344–354.
Messger S.L., McGuire J.A. 1998. Morphology, molecules, and the
phylogenetics of cetaceans. Syst. Biol. 47:90–124.
Milinkovitch M.C. 1997. The phylogeny of whales: a molecular ap-
approach. Soc. Mar. Mamm. (Spec. Publ) 3:317–338.
Milinkovitch M.C., Orti G., Meyer A. 1993. Revised phylogeny of
whales suggested by mitochondrial ribosomal DNA sequences. Nature. 361:346–348.
Miller K.G., Kominiz M.A., Browning J.V., Wright J.D., Mountain G.S.,
Katz M.E., Sugarman P., Cramer B.S., Christie-Blick N., Pekar S.F.
2005. The Panherozoic record of global sea-level change. Science. 310:1293–1298.
Muizon C.de 1988. Les relations phylogenetiques des Delphinidae
(Cetacea: Mammalia). Ann. Paleon. 74:159–227.
Sée N., Mooers A.O., Harvey P.H. 1992. Tempo and mode of evolution
revealed from molecular phylogenies. Proc. Natl. Acad. Sci. USA. 89:8322–8326.
Nicol S., Croxall J., Trathan P., Gales N., Murphy E. 2007. Paradigm
misplaced? Antarctic marine ecosystems are affected by climate
dome as well as biological processes and harvesting. Antarct. Sci. 19:291–295.
Nikaido M., Hamilton H., Makino H., Sasaki T., Takahashi K., Goto M.,
Kanda N., Pastene L.A., Okada N. 2006. Proceedings of the SMBE
Conference 
Kanda N., Pastene L.A., Okada N. 2006. Proceedings of the SMBE
Tri-National Young Investigators’ Workshop 2005. Baleen whale
Kanda N., Goto M., Kato H., Mcphee M.V., Pastene L.A. 2007. Benchmark data of a changing sea—paleoecogeography, paleobiogeography and events in the Central Paratethys during the Miocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 31:319–329.
Heyning J.E. 1997. Sperm whale phylogeny revisited: analysis of the morphological evidence. Mar. Mam. Sci. 13:596–613.
Ho S.Y.W., Phillips M.J. 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. Syst. Biol. 58:367–380.
Jain S., Collins L.S. 2007. Trends in Caribbean paleoproductivity re-
lated to the Neogene closure of the Central American Seaway. Mar. Micropaleontol. 63:57–74.
Kanda N., Goto M., Kato H., Mcphee M.V., Pastene L.A. 2007. Popu-
lational genetic structure of Bryde’s whales (Balaenoptera edeni) at the inter-oceanic and trans-equatorial levels. Conserv. Genet. 8:853–864.
Keane T.M., Creevey C.J., Pentony M.M., Naughton T.J., McLnerney J.O. 2006. Assessment of methods for amino acid matrix selection and their use on empirical data shows that ad hoc assumptions for choice of matrix are not justified. BMC Evol. Biol. 6:29.
Kuhnt W., Holbourn A., Hall R., Zueva M., Kase R. 2004. Neogene his-
tory of the Indonesian throughflow. In: Cliff P.D., editor. Continent-
ocean interactions within East Asian marginal seas. Washington (DC): American Geophysical Union. p. 1–22.
Lawrence K.T., Liu Z.H., Herbert T.D. 2006. Evolution of the eastern
tropical Pacific through Plio-Pleistocene glaciation. Science. 312:79–83.
Lear C.H., Bailey T.R., Pearson P.N., Coxall H.K., Rosenthal Y. 2008. Cooling and ice growth across the Eocene-Oligocene transition. Geology. 36:251–254.
Lear C.H., Rosenthal Y., Wright J.D. 2003. The closing of a seaway: ocean water masses and large climate change. Earth Planet. Sci. Lett. 210:425–436.
Livermore R., Hillenbrand C.D., Meredith M., Eagles G. 2007. Drake Passage and Cenozoic climate: an open and shut case? Geochem. Geophys. Geosyst. 8:1–11.
Luo Z., Gingerich P.D. 1999. Terrestrial Mesonychida to aquatic Cetacea: transformation of the basicranium and evolution of hearing in whales. University of Michigan Papers on Paleontology. 31:1–98.
Sanderson M.J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Mol. Biol. Evol. 19:101–109.
Sasaki T., Nikaido M., Hamilton H., Goto M., Kato H., Kanda N., Pastene L.A., Cao Y., Fordyce R.E., Hasegawa M., Okada N. 2005. Mitochondrial phylogenetics and evolution of mysticete whales. Syst. Biol. 54:77–90.
Scher H.D., Martin E.E. 2006. Timing and climatic consequences of the opening of Drake Passage. Science. 312:428–430.
Schluter D. 2000. The ecology of adaptive radiation. New York: Oxford University Press.
Shapiro B., Rambaut A., Drummond A.J. 2006. Choosing appropriate substitution models for the phylogenetic analysis of protein-coding sequences. Mol. Biol. Evol. 23:7–9.
Shevenell A.E., Kennett J.P., Lea D.W. 2008. Middle Miocene ice sheet dynamics, deep-sea temperatures, and carbon cycling: a Southern Ocean perspective. Geochem. Geophys. Geosyst. 9:Article Q02006.
Simpson G.G. 1953. The major features of evolution. New York: Columbia University Press.
Steeman M.E. 2007. Cladistic analysis and a revised classification of fossil and recent mysticetes. Zool. J. Linn. Soc. Lond. 150:875–894.
Thewissen J.G., editor. 1998. The emergence of whales: evolutionary patterns in the origin of Cetacea. New York: Plenum.
Thewissen J.G., Cooper L.N., Clementz M.T., Bajpai S., Tiwari B.N. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature. 450:1190–1194.
Thomas D.J., Via R.K. 2007. Neogene evolution of Atlantic thermo-haline circulation: perspective from Walvis Ridge, southeastern Atlantic Ocean. Paleoceanography. 22:Article PA2212.
Uhen M.D. 2008. New protocetid whales from Alabama and Mississippi, and a new cetacean clade, Pelagiceti. J. Vertebrae Paleontol. 28:589–593.
Uhen M.D., Pyenson N.D. 2005. Online Systematic Archive, Cetacea, The Paleobiology Database. Available from: http://paleodb.org/cgi-bin/bridge.pl?user=Guest&action=displayPage&page=OSA_9_Cetacea.
Uhen M.D., Pyenson N.D. 2007. Diversity estimates, biases, and historiographic effects: resolving cetacean diversity in the Tertiary. Palaeontol. Electronica. 10:11A:22.
Verma S.K., Sinha R.K., Singh L. 2004. Phylogenetic position of Platanista gangetica: insights from the mitochondrial cytochrome b and nuclear interphotoreceptor retinoid-binding protein gene sequence. Mol. Phylogenet. Evol. 33:280–288.
Weir J.T. 2006. Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. Evol. Int. J. Org. Evol. 60:842–855.
Williams S.T., Jara J., Gomez E., Knowlton N. 2002. The marine Indo-West Pacific break: contrasting the resolving power of mitochondrial and nuclear genes. Integr. Comp. Biol. 42:941–952.
Zachos J., Pagani M., Sloan L., Thomas E., Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science. 292:686–693.

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