Mitogenomic analyses provide new insights into cetacean origin and evolution

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Abstract

The evolution of the order Cetacea (whales, dolphins, porpoises) has, for a long time, attracted the attention of evolutionary biologists. Here we examine cetacean phylogenetic relationships on the basis of analyses of complete mitochondrial genomes that represent all extant cetacean families. The results suggest that the ancestors of recent cetaceans had an explosive evolutionary radiation 30–35 million years before present. During this period, extant cetaceans divided into the two primary groups, Mysticeti (baleen whales) and Odontoceti (toothed whales). Soon after this basal split, the Odontoceti diverged into the four extant lineages, sperm whales, beaked whales, Indian river dolphins and delphinoids (inid river dolphins, narwhals/belugas, porpoises and true dolphins). The current data set has allowed test of two recent morphological hypotheses on cetacean origin. One of these hypotheses posits that Artiodactyla and Cetacea originated from the extinct group Mesonychia, and the other that Mesonychia/Cetacea constitutes a sister group to Artiodactyla. The current results are inconsistent with both these hypotheses. The findings suggest that the claimed morphological similarities between Mesonychia and Cetacea are the result of evolutionary convergence rather than common ancestry.

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1. Introduction

The order Cetacea traditionally includes three suborders: the extinct Archaeoceti and the recent Odontoceti and Mysticeti. It is commonly believed that the evolution of ancestral cetaceans from terrestrial to marine (aquatic) life was accompanied by a fast and radical morphological adaptation. Such a scenario may explain why it was, for a long time, difficult to morphologically establish the position of Cetacea in the mammalian tree and even to settle whether Cetacea constituted a monophyletic group.

Biochemical analyses in the 1950s (Boyden and Geme-roy, 1950) and 1960s (Goldstone and Smith, 1966) had shown a closer relationship between cetaceans and artiodactyls (even-toed hoofed mammals) than between cetaceans and any other eutherian order and karyological studies in the late 1960s and early 1970s unequivocally supported cetacean monophyly (Arnason, 1969, 1974). The nature of the relationship between cetaceans and artiodactyls was resolved in phylogenetic studies of mitochondrial (mt) cytochrome b (cytb) genes (Irwin and Arnason, 1994; Arnason and Gullberg, 1996) that placed Cetacea within the order Artiodactyla itself as the sister group of the Hippopotamidae (see also Sarich, 1993). The Hippopotamidae/Cetacea relationship was subsequently supported in studies of nuclear data (Gatesy et al., 1996; Gatesy, 1997) and statistically established in analysis of complete mt genomes (Ursing and Arnason, 1998). The relationship has also been confirmed in analyses of combined nuclear and mt sequences (Gatesy et al., 1999; Cassens et al., 2000) and in studies of short interspersed repetitive elements (SINEs) (Nikaido et al., 1999, 2001). Artiodactyla and Cetacea are now commonly referred to as Cetartiodactyla (Montgelard et al., 1997).

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Abbreviations: aa, amino acid(s); bp, base pair(s); cytb, gene encoding cytochrome b; LBP, local bootstrap probability; ML, maximum likelihood; MP, maximum parsimony; mt, mitochondrial; MYBP, million years before present; NJ, neighbor joining; nt, nucleotide(s); PCR, polymerase chain reaction; QP, quartet puzzling; SINEs, short interspersed repetitive elements.
Similarly, Cetruminantia (Ursing and Arnason, 1998) refers to the assembly of Ruminantia and Cetacea/Hippopotamidae, while Cetancodonta (Arnason et al., 2000) encompasses Cetacea and Hippopotamidae.

Previous analyses of the complete cytb gene of more than 30 cetacean species (Arnason and Gullberg, 1996) identified five primary lineages of recent cetaceans, viz., Mysticeti and the four odontocete lineages Physeteridae (sperm whales), Platanistidae (Indian river dolphins), Ziphiidae (beaked whales) and Delphinidae (inid river dolphins, porpoises, narwhals and dolphins). However, these studies left unresolved the relationships of the five lineages as well as those between the three delphinoid families Monodontidae (narwhals, belugas), Phocoenidae (porpoises) and Delphinidae (dolphins). Therefore, the relationships between the four mysticete families Balaenopteridae (right whales), Neobalaenidae (pygmy right whales), Eschrichtiidae (gray whales) and Balaenopteridae (rorquals) were not conclusively resolved in analyses of cytb genes (Arnason and Gullberg, 1994, 1996). Here we examine all these relationships based on mitogenomic analyses, i.e. analyses of mt genomes that have been sequenced in their entirety. To this end, the mt genomes of four mysticetes and nine odontocetes have been added to the preexisting data set of the fin whale, the pygmy sperm whale, the grey whale, Hyperoodon ampullatus and the N. Atlantic minke whale, Balaenoptera acutorostrata (Balaenopteridae, AJ554054). The nine odontocetes are the pygmy sperm whale, Kogia breviceps (Physeteridae, AJ554055); the bottlenose whale, Hyperoodon ampullatus (AJ554056) and the Baird’s beaked whale, Berardius bairdii (AJ554057) of the family Ziphiidae; the Indian river dolphin, Platanista minor (Platanistidae, AJ554058); the Amazon dolphin, Inia geoffrensis (AJ554059) and the La Plata dolphin, Pontoporia blainvillei (AJ554060) (Iniidae), the white-beaked dolphin, Lagenorhynchus albirostris (Delphinidae, AJ554061), the narwhal, Monodon monoceros (Monodontidae, AJ554062) and the harbour porpoise, Phocoena phocoena (Phocoenidae, AJ554063). The Iniidae, the Monodontidae and the Phocoenidae are commonly included in the superfamily Delphinidea. The accession number of the new mt genome of the alpaca is AJ566364. The organisation of the new genomes conforms to the general eutherian pattern. In addition to the 14 new genomes, the data set includes the fin whale, Balaenoptera physalus (Balaenopteridae, X61145), the blue whale, Balaenoptera musculus (Balaenopteridae, X72204) and the sperm whale (Physeteridae, AJ277029), and the six artiodactyls: cow, Bos taurus (J01394), sheep, Ovis aries (AF010406), muntjac, Muntiacus muntjac (AY225986), pig, Sus scrofa (AJ002189) and hippopotamus, Hippopotamus amphibius (AJ010957). The cetartiodactyl tree was rooted with four perissodactyls: horse, Equus caballus (X79547), donkey, Equus asinus (X97337), Indian rhinoceros, Rhinoceros unicornis (X97336) and white rhinoceros, Ceratotherium simum (Y07726).

2. Materials and methods

2.1. The mitogenomic data set

The 13 new cetacean mt genomes and the new mt genome of the alpaca were PCR-amplified in 2–5 kb large fragments using Ex-Taq DNA polymerase and conserved primers that were established on the basis of the mt sequences of the fin (Arnason et al., 1991a), blue (Arnason and Gullberg, 1993) and sperm (Arnason et al., 2000) whales and the previously reported sequence of the alpaca (Ursing et al., 2000). The PCR products were purified by ultrafiltration (Millipore) and sequenced employing an ABI or a LICOR-4000L system. The four mysticetes are the bowhead, Balaena mysticetus (family Balaenidae, accession number AJ554051); the pygmy right whale, Caperea marginata (Neobalaenidae, AJ554052); the grey whale, Eschrichtius robustus (Eschrichtiidae, AJ554053); and the N. Atlantic minke whale, Balaenoptera acutorostrata (Balaenopteridae, AJ554054). The nine odontocetes are the pygmy sperm whale, Kogia breviceps (Physeteridae, AJ554055); the bottlenose whale, Hyperoodon ampullatus (AJ554056) and the Baird’s beaked whale, Berardius bairdii (AJ554057) of the family Ziphiidae; the Indian river dolphin, Platanista minor (Platanistidae, AJ554058); the Amazon dolphin, Inia geoffrensis (AJ554059) and the La Plata dolphin, Pontoporia blainvillei (AJ554060) (Iniidae), the white-beaked dolphin, Lagenorhynchus albirostris (Delphinidae, AJ554061), the narwhal, Monodon monoceros (Monodontidae, AJ554062) and the harbour porpoise, Phocoena phocoena (Phocoenidae, AJ554063). The Iniidae, the Monodontidae and the Phocoenidae are commonly included in the superfamily Delphinidea. The accession number of the new mt genome of the alpaca is AJ566364. The organisation of the new genomes conforms to the general eutherian pattern. In addition to the 14 new genomes, the data set includes the fin whale, Balaenoptera physalus (Balaenopteridae, X61145), the blue whale, Balaenoptera musculus (Balaenopteridae, X72204) and the sperm whale (Physeteridae, AJ277029), and the six artiodactyls: cow, Bos taurus (J01394), sheep, Ovis aries (AF010406), muntjac, Muntiacus muntjac (AY225986), pig, Sus scrofa (AJ002189) and hippopotamus, Hippopotamus amphibius (AJ010957). The cetartiodactyl tree was rooted with four perissodactyls: horse, Equus caballus (X79547), donkey, Equus asinus (X97337), Indian rhinoceros, Rhinoceros unicornis (X97336) and white rhinoceros, Ceratotherium simum (Y07726).

2.2. Phylogenetic analysis

The phylogenetic analyses were carried out at both the amino acid (aa) and nucleotide (nt) levels, using the concatenated sequences of 12 mt protein-coding genes, excluding the NADH6 gene, the composition of which differs from that of other mt protein-coding genes. The analyses were performed employing distance, parsimony and maximum likelihood methods. The mtREV-24 model of aa sequence evolution and the TN-93 model of nt evolution were used for distance and likelihood analyses. Phylogenetic reconstruction was performed under the assumptions of both rate homogeneity and rate heterogeneity among sites, the latter with a Γ model with eight classes of variable sites. Likelihood values, standard deviations, bootstrap support values and the number of substitutions and their standard deviations were used for comparison of alternative trees. Divergence times were estimated using a smoothing factor of 3 as estimated according to Sanderson (2002).
3. Results and discussion

3.1. Phylogenetic relationships

Fig. 1 shows cetartiodactyl relationships as identified in maximum likelihood (ML) analysis of the aa data set. Despite the substantial size of the data set, resolution in some parts of the tree was limited, suggesting that several divergences had taken place within a narrow temporal window. The results of a comparison between the tree in Fig. 1 and some alternative topologies are given in Table 1.

All analyses identified monophyletic Cetruminantia, Cetancodonta and Cetacea, but the relationship between Suina, Tylopoda and Cetruminantia was not conclusively resolved [cf. Table 1, topology (a) versus topologies (b) and (c)]. A basal split between Tylopoda and remaining cetartiodactyls has been favoured in some previous molecular studies, and one SINE diagnostic for that relationship has been identified (Nikaido et al., 1999). That tree (b) was not the preferred one in the current analyses, however.

The cetacean branch extending from the hippopotamid/cetacean split to the basal split among recent cetaceans is long. The ML analyses identified monophyletic Mysticeti and Odontoceti, but the common odontocete branch is short. Within the Mysticeti, the basal split between Balaenidae and the branch encompassing Neobalaenidae, Eschrichtiidae and Balaenopteridae is consistent with sequence analyses of the common cetacean DNA satellite (Arnason et al., 1992), mysticete control regions (Arnason et al., 1993a) and cytb genes (Arnason and Gullberg, 1994, 1996). It is also congruent with the organisation and sequence data of the heavy mysticete DNA satellite (Adegoke et al., 1993) and...
the presence of the light DNA satellite in Neobalaenidae, Eschrichtiidae and Balaenopteridae versus its absence in the Balaenidae (Arason and Best, 1991).

The branch joining Neobalaenidae/Eschrichtiidae/Balaenopteridae is short and the favoured topology was not strongly supported [cf. topology (d) versus the best tree]. The phylogenetic position of the Eschrichtiidae has been contentious (Barnes and McLeod, 1984), and some morphological analyses have placed it as a basal mysticete lineage. However, molecular analyses have, in general, registered a close relationship between Eschrichtiidae and Balaenopteridae (Arnason et al., 1992; Adegase et al., 1993; Arason and Gullberg, 1994). Some of these analyses have even placed the grey whale within the Balaenopteridae, albeit with inconclusive support. The current aa data set supported a position of Eschrichtiidae outside the Balaenopteridae [Table 1 (e), but some nt trees placed it within the Balaenopteridae, inside the position of the minke whale].

The branches separating the four odontocete lineages are short and their positions, therefore, are not conclusively defined. The rate homogeneity tree in Fig. 1 has Platanistidae and Delphinoidea as sister groups, although topology (f), a sister group relationship between Ziphiidae and Delphinoidea, is not refuted. Rate heterogeneity analysis favours topology (f), but the support for the second best topology (a) is essentially the same. Topology (f) is consistent with a recent study of SINEs (Nikaido et al., 2001).

A sister group relationship between Mysticeti (actually Balaenopteridae) and Physeteridae has been advocated in some molecular studies (Milinkovitch et al., 1993). However, disruption of odontocete monophyly by joining Mysticete and Physeteridae on a common branch (topology g) is not supported by the mitogenic data set. Topology (h) joins Physeteridae and Ziphiidae as sister groups. This hypothesis, Physeterida (de Muizon, 1991), is not favoured by the mitogenic results.

Traditional river dolphins (Indian river dolphins + inuids) split into two distinct lineages, Platanistidae and Inuidae, with the Inuidae falling within the Delphinoidea. Monophyly of traditional river dolphins was conclusively refuted [cf. topology (j) versus the best tree]. Molecularly, this relationship was originally demonstrated in analyses of cytb genes (Arnason and Gullberg, 1996). That finding was congruent with some earlier morphological views (de Muizon, 1988; Heyning, 1989; Heyning and Mead, 1990) but inconsistent with the general morphological understanding at the time. The paraphyly of river dolphins has been reinforced more recently in studies using other molecular data (Cassens et al., 2000; Hamilton et al., 2001; Nikaido et al., 2001).

Some nt analyses placed Delphinoidea as the sister group of all other cetaceans. That topology (i) is incongruent with the aa analyses, however. The molecular evolution of the two inuids, I. Geoffreanis and P. Blainvillei, is faster than that of other cetaceans, and removal of these two species from the data set reduces the tendency for a basal position of the Delphinoidea in the nt tree. Within the Delphinoidea, the analyses identified Monodontidae and Phocoenidae as sister groups to the exclusion of Delphinidae [Fig. 1, branch H; see also Table 1, topologies (k) and (l) versus the best trees].

The karyotypes of many cetaceans, e.g. the balaenopterids (Arnason, 1974) and the odontocete killer whale (Arnason et al., 1980), have conspicuous C-band positive regions, i.e. made up of constitutive heterochromatin. Most of these regions harbour the so-called common cetacean DNA satellite which occurs in all cetaceans, both odontocetes and mysticetes. The repeat length of the satellite is ~1750 bp in all cetaceans except the Delphinidae in which the repeat length is ~1580 bp (Arnason et al., 1984). The current phylogenetic results confirm the notion that the ~1580-bp repeat is a delphinid synapomorphy. For the discussion of delphinid relationships in general, it is of interest that the Irrawaddy dolphin, Orcaella brevirostris, which some authors have included in the Monodontidae on morpholog-
chal grounds, is characterized by the \( \approx 1580\)-bp repeat (Gretarsdottir and Arnason, 1992). That synapomorphy and the analyses of the cytB gene conclusively place Orcella within the Delphinidae. For further discussion of mt relationships within the Ziphiidae and the Delphinidae, the reader should consult the more speciose cytB study of Arnason and Gullberg (1996).

The limited molecular resolution among basal cetacean lineages has been known for some time. Studies of haemoglobin and myoglobin (Goodman, 1989; Czelusniak et al., 1990) have either joined Physeteridae and Mysticeti to the exclusion of Delphinoida (myoglobin data) or Mysticeti and Delphinoida to the exclusion of Physeteridae (haemoglobin data). Thus, neither of the data sets identified monophyletic Odontoceti by joining the two odontocete lineages (Physeteridae and Delphinoida) to the exclusion of Mysticeti. A similar instability was recognized and cautioned against in analyses of some mt data, notably, sequences of rRNA genes (Arnason et al., 1993b). The suggestion (Milinkovitch et al., 1993) of a sister group relationship between Physeteridae and the mysticete family Balaenopteridae (rorquals) was based on a myoglobin data set (which joins Physeteridae and Mysticeti to the exclusion of Delphinoida) that was complemented with partial data of the mt 16S rRNA gene. The authors also calculated that the physeterid/orcaual divergence had taken place as recently as 10–13 million years before present (MYBP), a dating that is incompatible with both physeterid and mysticete palaeontology. The rRNA data underlying the proposal for a close physeterid/balaenopterid relationship have been independently realigned by other authors (Cerchio and Tucker, 1998; Messen-ger and McGuire, 1998). Analysis of the realigned data set erased the support for the particular orcaual/physeterid relationship (see also Ohland et al., 1995; Heyning, 1997; Luckett and Hong, 1998). Similarly, neither analyses of SINEs (Nikaido et al., 2001) nor the current results support this particular relationship or evolutionary hypotheses (e.g. Milinkovitch, 1995) that have been based on it.

3.2. Divergence times

Previous analyses of cetacean and artiodactyl/cetacean relationships have led to the construction of two molecular/palaeontological calibration points (references) that have come into general use for estimating the times of various divergences in the mammalian tree (e.g. Arnason and Janke, 2002). These references are A/C-60, which relates to a divergence between ruminant artiodactyls and cetaceans 60 MYBP (Arnason and Gullberg, 1996; Arnason et al., 1996), and O/M-33, which is based on the divergence (\( \approx 33 \) MYBP) between the five primary lineages of extant cetaceans (Arnason and Gullberg, 1996; Arnason et al., 2000). Here we place the O/M calibration point at 35 MYBP rather than at 33 MYBP. This change is in accord with the Eocene/Oligocene age of Llanocetus (Mitchell, 1989; Fordyce and de Muizon, 2001), the oldest mysticete fossil found so far. Both references yield molecular estimates that show general consistency with mammalian palaeontology (Arnason et al., 2000, 2002; Arnason and Janke, 2002).

The cetacean divergence times calculated using A/C-60 and O/M-35 as references have been included in Fig. 1. As a result of the short branches separating several cetacean lineages, the estimates of these divergences overlap. The same observation has been made in calculations based on SINE flanking sequences (Nikaido et al., 2001). There is a general consistency between the current and the flanking sequence datings, except for those involving the Balaenopteridae, which are somewhat younger in our analysis than in the SINEs study. The currently estimated age of the divergence between Hippopotamus and Cetacea (\( \approx 53.5 \) MYBP) is consistent with the age (>50 MY) of the oldest archaeocete fossils identified so far (Bajpai and Gingerich, 1998). This suggests that the ages allocated to the two references, A/C-60 (the divergence between ruminant artiodactyls and cetaceans) and O/M-35 (the divergence between odontocetes and mysticetes) are reasonably accurate.

The dating of the divergence between the blue and fin whales is of interest regarding hybridization between closely related mammalian species. Previous molecular analyses (Arnason et al., 1991b; Spilliaert et al., 1991) demonstrated the occurrence of hybridization between these two species. These studies, which were based on three hybrids (one female and two males), showed that either species could be the mother or father in these hybridizations. The two male hybrids had rudimentary testes, whereas the female hybrid was in her second pregnancy. This suggests that the blue and fin whales may be close to the limit for permissible species hybridization among mammals.

3.3. Morphological hypotheses in the light of the current results

The current data set has allowed examination of the coherence between the molecular results and two prevalent morphological hypotheses related to cetacean evolution. The first hypothesis, which in essence originates from Van Valen (1966, 1968), postulates that monophyletic Artiodactyla and monophyletic Cetacea evolved separately from the extinct Palaeocene group Mesonychia. This hypothesis was recently reinforced in a morphological study (Thewissen et al., 2001) that included mesonychians, two archaeocete taxa (Ambulocetus and Pakicetus) and some extant fossil artiodactyls. The study of Thewissen et al. (2001) showed a sister group relationship between monophyletic Artiodactyla and monophyletic Cetacea, with Mesonychia as the basal sister group of Artiodactyla/Cetacea, a conclusion consistent with the palaeontological age of Mesonychia relative to that of Artiodactyla and Cetacea. The second hypothesis favours a sister group relationship between Mesonychia and Cetacea with the Mesonychia/Cetacea clade as the sister group of monophyletic Artiodactyla (O’Leary and Geisler, 1999; see also Gatesy and O’Leary, 2001). The palaeontological age of
the Mesonychia, which exceeds that of the artiodactyls, is an additional complication for the second (O’Leary and Geisler, 1999) hypothesis, however.

Although the position of Mesonychia differs in the two morphological hypotheses, both correspond to a sister group relationship between Cetacea and monophyletic Artiodactyla among extant cetartiodactyls. Thus, both hypotheses can be tested against the current data set. The result of such a test has been included in Table 1, topology (m). As evident, both these morphological hypotheses are incongruent with the mitogenomic findings.

The data set upon which the hypothesis of O’Leary and Geisler (1999) rests was reanalysed by Naylor and Adams (2001). The reanalysis showed that the data set used by O’Leary and Geisler (1999) was heterogeneous in regard to basicranial and dental partitions. The basicranial partition had little influence on the tree. However, exclusion of the dental partition had a pronounced effect, as it resulted in a tree that disrupted the connection between Mesonychia and Cetacea, instead placing Mesonychia as a basal sister group of Artiodactyla/Cetacea. In addition, Artiodactyla became paraphyletic with the Hippopotamidae as the cetacean sister of Artiodactyla/Cetacea. In addition, Artiodactyla became paraphyletic with the Hippopotamidae as the cetacean sister group among recent artiodactyls. As suggested by Naylor and Adams (2001), it is probable that the pronounced influence of dental characters on the morphological data set reflects multiple coding of the same features. The tree reconstructed in the morphological reanalysis is essentially the same as the mitogenomic tree, except for the position of Camelus, which fell among the Ruminantia in Naylor and Adams’s (2001) study.

Morphological studies have not provided an answer to the question whether mysticetes and odontocetes had separate origins among the archaeocetes (Fordyce and de Muizon, 2001). However, the long common cetacean branch and the short branches separating the five extant cetacean lineages strongly suggest an origin of modern cetaceans from the same archaeocete group (probably the Dorudontidae).

Basal cetartiodactyl relationships were recently examined in the light of two new fossil cetaceans, Artiocetus clavis and Rodhocetus balochistanensis (Gingerich et al., 2001). As discussed by the authors, the five-fingered hand of Rodhocetus resembles the primitive hand condition found in the oldest-known artiodactyls and in the palaentologically somewhat younger anthracotheriids. The potential anthracotheriid/hippopotamid connection was discussed by Amason et al. (2000) in the light of the molecular sister group relationship between Hippospadae and Cetacea (the Cetancodonta hypothesis). As discussed by Colbert (1935), the anthracotheriids showed in the upper Tertiary numerous structural characters strongly suggestive of the Hippopotamidae. Colbert did not consider the possibility of a connection between these two groups and Cetacea, however.

The current results are inconsistent with morphological views that place cetacean origin outside extant Artiodactyla. It is also problematic to reconcile the Palaeocene age of the oldest mesonychid fossils with morphological conclusions that suggest a sister group relationship between Mesonychia and Cetacea within paraphyletic Artiodactyla. Recent morphological analyses (Gingerich et al., 2001; Naylor and Adams, 2001) have disrupted the morphologically claimed relationship between Mesonychia and Cetacea. Congruity between molecular and morphological findings has thus been achieved. The current findings support that the claimed morphological similarities between Mesonychia and Cetacea are the result of evolutionary convergence rather than common ancestry (Gingerich et al., 2001). It will be interesting to follow if forthcoming morphological analyses will clarify whether the discordance between the molecular results and morphological conclusions that place cetacean origin outside the Artiodactyla is related to a confusion of mesonychid and archaeocete taxa.

The importance of Ambulocetus for morphologically deciphering cetacean evolution has been stressed in some recent accounts. Thus, de Muizon (2001) stated that these fossils “should take their place among other famous ‘intermediates’, such as the most primitive bird, Archaeopteryx, and the early hominid Australopithecus.” Letting alone that Australopithecus has been replaced by Orrorin (Senut et al., 2001) as the currently described oldest hominid with upright gait, it is worrisome that such an outstanding fossil as Ambulocetus did not permit resolution of the now commonly acknowledged sister group relationship between Hippopotamidae and Cetacea.

The limbs of Ambulocetus constitute somewhat of an evolutionary enigma. As evident in Thewissen et al.’s (1994) paper, Ambulocetus has very large hind limbs compared to its forelimbs, a difference that is less pronounced in later silhouette drawings of the animal. It is nevertheless evident that evolution from the powerful hindlimbs of Ambulocetus to their rudimentation in archaeocetes constitutes a remarkable morphological reversal if Ambulocetus is connected to the cetacean branch after the separation of the hippopotamid and cetacean lineages.

3.4. Evolutionary relationships and systematic nomenclature

For natural reasons, systematic schemes have traditionally been based on external morphological characteristics. The rates of morphological and molecular evolution are rarely (if ever) strictly correlated, however, and this may give rise to inconsistency between traditional systematics and molecular findings. The emerging consensus that the order Cetacea resides within another traditional order, Artiodactyla, makes apparent the incongruity in cetartiodactyl nomenclature (Graur and Higgins, 1994). In this instance, a possible solution for maintaining reasonable consistency between nomenclature and phylogeny would be to recognize Cetartiodactyla as an order with three suborders: Suina, Tylopoda and Cetruminantia. According to such a scheme, Cetacea would (together with the Hippopotamidae) constitute a parvorder within the infraorder Cetancodonta. However, the
difficulties in joining morphological and molecular phylogenetic schemes are patently underlined by the fact that the origin of the Cetartiodactyla would still be considerably more recent than the age of some subordinal divergences within the order Rodentia. For discussion of the coherence (or rather the general lack thereof) between classification, phylogeny and nomenclature, the reader should consult Benton (2000).

3.5. Conclusions

(1) The complete mt genomes of 13 cetacean species, representing all extant families, were sequenced.
(2) Together with three previously sequenced cetacean genomes and a number of artiodactyl genomes, the data were used to phylogenetically examine various cetartiodactyl relationships.
(3) The analyses identified three basal cetartiodactyl lineages: Suina (pig), Tylopoda (alpaca) and Cetrumi
niantia. Cetrumiiniantia splits into Ruminantia (cow, sheep and muntjac) and Catcandodonta (hippopotamus and cetaceans).
(4) The sister group relationship between Hippopotomidae and Cetacea was strongly supported. The divergence between these two lineages was estimated to have taken place 53–54 MYBP, an estimate that is consistent with the oldest archaeocete fossils found so far.
(5) Within Cetacea, a basal split between Odontoceti and Mysticeti was identified. Odontoceti split into four basal lineages. Relationships among these lineages were poorly resolved, suggesting that these splits had taken place within a narrow temporal window ≈ 30 MYBP.
(6) The molecular results are inconsistent with two recent morphological hypotheses on cetacean origin that have postulated a close relationship between Cetacea and the extinct group Mesonychia.

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