



Diverse stem cetaceans and their phylogenetic relationships with mesonychids and artiodactyls

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Abstract The transition in the evolution of cetaceans from terrestrial life to a fully aquatic existence is one of the most enduring evolutionary mysteries. Stem cetaceans are quite diverse and well documented in the fossil record. Five family level clades form the paraphyletic stem cetaceans ('archaeocetes'): Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae. The most basal group, the pakicetids probably had a semi-aquatic life, living near the freshwater environment. They likely represent the initial step in the transformation of a terrestrial artiodactyl to an aquatic cetacean. The more derived ambulocetids exhibit more characters likely linked to increasing aquatic adaptation, and they probably were more adapted to the marine realm than to a freshwater environment. Remingtonocetids show evolution of balance organs and the sound transmission mechanism in the direction of modern cetaceans. Stable oxygen isotope analyses suggest that remingtonocetids were probably exclusively marine. Protocetids are very diverse, and they are the first cetacean group that acquired a global distribution. Protocetids retain well-developed hind limbs, but their pelvic-vertebra articulation became loose or completely lost. Basilosaurids are the extinct sister group to the crown cetaceans. The phylogenetic relationships between cetaceans and other mammals have long been debated. Molecular, paleontological, and morphological data and analyses all support a close evolutionary link between cetaceans and artiodactyls. However, the prevalent hippopotamus-cetacean hypothesis does not receive solid support from paleontological and morphological data. Detailed review and more extensive phylogenetic analyses on anthracotheriids and entelodontids will aid the clarification of uncertainties related to the hippopotamus-cetacean phylogenetic hypothesis. If the phylogenetic positions of extant cetaceans and artiodactyls were not constrained by molecular data, the traditional mesonychid-cetacean relationship would still have support from the analyses based solely on paleontological and morphological data.

Key words Archaeoceti, Artiodactyla, Mesonychidae, hippopotamus, phylogeny

1 Introduction

The members of the Order Cetacea include the commonly known whales, dolphins,

中国科学院战略性先导科技专项(编号: XDB03020501)、国家重点基础研究发展计划项目(编号: 2012CB821904)和中国科学院百人计划资助。

收稿日期: 2014-05-28

and porpoises. They represent a major division of mammals adapted to living in an aquatic, largely marine environment. The origin of cetaceans and the phylogenetic relationship between cetaceans and other mammals have been studied, discussed, and debated for over a century. In recent years, new molecular data added scrutiny on cetacean origins, disrupted the classic view based on fossils and morphology, and place extant cetaceans as the sister group of hippopotamus, nested within the artiodactyls. Here we review the discoveries of the basal cetaceans, their impact on the understanding of the origin of cetaceans, and the recent arguments about the phylogeny of cetaceans and other mammals based on phenotypic and molecular data.

2 Biology of cetaceans

Extant cetaceans appear to be very different from the “typical” mammals. Presence of fur and external pinna are two obvious mammalian plesiomorphies, but extant cetaceans have none of them. They have a body-plane generally similar to other marine vertebrates, such as fishes and ichthyosaurs. Their forelimbs evolved into fin-like flippers with no visible digits, and their hind limbs have been lost completely. Only vestigial and unattached pelvic bones are present in mysticetes and some male odontocetes, serving as an anchor for the muscles of the penis (Slijper, 1962). The tails of cetaceans all have been changed into the mediolaterally wide whale flukes, differing from the dorsoventrally expanded fins of fish, ichthyosaurs, mosasaurs, and other marine vertebrates. Many species also have dorsal fins. On the other hand, cetaceans are endothermic, possess a neocortex, and have three middle ear bones, and females have mammary glands and form a placenta during reproduction. All these features are plesiomorphies of placental mammals, and a combination of these features clearly distinguishes placental mammals from all the other vertebrates (Slijper, 1962; Fordyce and Barnes, 1994; Thewissen and Williams, 2002; Thewissen et al., 2009; Uhen, 2010).

The Order Cetacea is divided into three suborders: the paraphyletic archaic whale Archaeoceti, the monophyletic baleen whales Mysticeti, and the monophyletic toothed whales Odontoceti (Slijper, 1962; Fordyce and Barnes, 1994; Rice, 1998; Thewissen and Williams, 2002; Thewissen et al., 2009; Uhen, 2010). The members of suborder Archaeoceti are all extinct species forming the stem group leading to crown Cetacea, mostly being primitive whales that inhabited Eocene aquatic environments. Crown Cetacea is formed of Mysticeti and Odontoceti. The ancestral forms of mysticetes and odontocetes appeared in the transitional period between the Eocene and Oligocene, and flourished thereafter (Fordyce, 1989, 2003; Fordyce and Barnes, 1994; Fordyce and Muizon, 2001; Uhen, 2010).

While extant cetaceans may not be specifically diverse (89 species), they are morphologically diverse, reflected in the 14 familial level taxa (Steeman et al., 2009). The Blue whale (*Balaenoptera musculus*), a species of rorquals (literally mean furrow whales, a reference to the longitudinal folds of skin below the mouths of this group), is widely known

as the largest extant animal with a body length up to 30 meters and a body mass of nearly 150 tons (Sears and Calambokidis, 2002). In contrast, the vaquita (*Phocoena sinus*), a critically endangered species distributed in an extremely limited geographic range in the northern part of the Gulf of California, is the smallest extant cetacean. Its body length is less than 1.5 meters, with a body mass less than 50 kg (Hohn et al., 1996). Most of the cetaceans inhabit in the ocean. However six species, the Amazon dolphin (*Inia geoffrensis*), *I. araguaiaensis*, *I. boliviensis*, the Ganges dolphin (*Platanista gangetica*), *Pontoporia blainvillei*, and the recently extinct Baiji dolphin (*Lipotes vexillifer*) are confined to freshwater environment. These six taxa are collectively called river dolphins, but they do not share a common ancestor (Rice, 1998).

The two main clades within the crown group of whales are highly distinct from each other. Mysticetes are usually larger than the odontocetes. The crania of the former are symmetrical, with two blowholes (external naris). Adult mysticetes bear no teeth, but instead have keratinous baleen plates. Baleen is bristle-like structure used for filtering small marine animals, such as krill, copepods and small fishes. Although it is also known as whalebone, baleen actually is not made of osseous tissue, but of keratin. Odontocetes usually have beak-like snout. As their name suggests, the beak-like snouts of odontocetes bear true teeth, which are single-rooted and usually numerous, an adaptation for catching fish, squid, and other marine animals. The skulls of odontocetes are usually asymmetrical, as a part of the osteological modification to their echolocation behavior. On top of their heads, odontocetes all bear rounded lens-shaped melons and single blowholes. The melon consists of low-density wax-like lipids that propagate the sound pulse and also serve as an acoustic lens focusing the directional sound beams.

The significant anatomical differences between mysticetes and odontocetes induced many researchers to believe that the two groups did not share the same common ancestor and evolved from different terrestrial groups (Miller, 1923; Yablokov, 1965; Jefferson et al., 1993). Now it is widely accepted that three suborders of Cetacea form a monophyletic group (Fordyce and Barnes, 1994; Luo and Gingerich, 1999; Thewissen and Williams, 2002; Rose, 2006; Thewissen et al., 2009; Uhen, 2010).

3 Diverse archaeocetes

It is generally accepted that Suborder Archaeoceti is a paraphyletic assemblage. Five families were lumped in this suborder (Table 1): Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae and Basilosauridae (Thewissen and Williams, 2002; Rose, 2006; Thewissen et al., 2009; Uhen, 2010). However, this system is not without controversy. Some researchers treat Pakicetidae and Ambulocetidae as subfamilies of Protocetidae (Fordyce and Barnes, 1994; McKenna and Bell, 1997). The Family Basilosauridae is subdivided into three subfamilies: Basilosaurinae, Dorudontinae and Stromeriinae (Uhen, 2004, 2010). The subfamily Dorudontinae sometimes is regarded as a separate family (Fordyce and Barnes,

Table 1 Classification of archaeocetes at genus level

Order Cetacea Brisson, 1762

Suborder Archaeoceti Flower, 1883

Family Pakicetidae Gingerich & Russell, 1990

Ichthyolestes Dehm & Oettingen-Spielberg, 1958

Nalacetus Thewissen & Hussain, 1998

Pakicetus Gingerich & Russell, 1981

Family Ambulocetidae Thewissen, Madar & Hussain, 1996

Ambulocetus Thewissen, Hussain & Arif, 1994

Gandakasia Dehm & Oettingen-Spielberg, 1958

Himalayacetus Bajpai & Gingerich, 1998

Family Remingtonocetidae Kumar & Sahni, 1986.

Andrewsiphius Sahni & Mishra, 1975

Attockicetus Thewissen & Hussain, 2000

Dalanistes Gingerich, Arif & Clyde, 1995

Kutchicetus Bajpai & Thewissen, 2000

Remingtonocetus Kumar & Sahni, 1986

Family Protocetidae Stromer, 1908

Subfamily Georgiacetinae Gingerich, Zalmout, Ul-Haq & Bhatti, 2005

Babiacetus Trivedy & Satsangi, 1984

Carolinacetus Geisler, Sanders & Luo, 2005

Crenatocetus McLeod & Barnes, 2008

Eocetus Fraas, 1904

Georgiacetus Hulbert, Petkewich, Bishop, Bukry & Aleshire, 1998

Natchitochia Uhen, 1998

Pappocetus Andrews, 1920

Pontobasileus Leidy, 1873

Subfamily Protocetinae Stromer, 1908

Aegyptocetus Bianucci & Gingerich, 2011

Artiocetus Gingerich, Ul-Haq, Zalmout, Khan & Malkani, 2001

Gaviacetus Gingerich, Arif & Clyde, 1995

Indocetus Sahni & Mishra, 1975

Maiiacetus Gingerich, Ul-Haq, Koenigswald, Sanders, Smith & Zalmout, 2009

Protocetus Fraas, 1904

Qaisracetus Gingerich, Ul-Haq, Khan & Zalmout, 2001

Rodhocetus Gingerich, Raza, Arif & Anwar, 1994

Takracetus Gingerich, Arif & Clyde, 1995

Togocetus Gingerich & Cappetta, 2014

Subfamily Makaracetinae Gingerich, Zalmout, Ul-Haq & Bhatti, 2005

Makaracetus Gingerich, Zalmout, Ul-Haq & Bhatti, 2005

Family Basilosauridae Cope, 1868

Subfamily Basilosaurinae Cope, 1868

Basilosaurus Harlan, 1834

Basiloterus Gingerich, Arif, Bhatti, Anwar & Sanders, 1997

Basilotritus Goldin & Zvonok, 2013

Subfamily Dorudontinae Miller, 1923

Ancalocetus Gingerich & Uhen, 1996

Chrysocetus Uhen & Gingerich, 2001

Cynthiacetus Uhen, 2005

Dorudon Gibbes, 1845

Masracetus Gingerich, 2007

Ocucajea Uhen, Pyenson, Devries, Urbiba & Renne, 2011

Saghacetus Gingerich, 1992

Supayacetus Uhen, Pyenson, Devries, Urbiba & Renne, 2011

Zygorhiza True, 1908

Subfamily Stromeriinae Gingerich, 2007

Stromerius Gingerich, 2007

1994). All archaeocetes are from the Eocene, and they are diverse with 43 genera reported, compared to the roughly 40 genera of extant cetaceans (Gingerich, 2005). The geographic distribution of these early whales is not as wide as that of the extant cetaceans with most of the fossils having been discovered in the coastal region of the old Tethys Seaway, in modern Pakistan, India, and Egypt. Although, some taxa are known from Nigeria and North America (Gingerich, 2005; Rose, 2006; Uhen, 2010).

3.1 Pakicetidae

The oldest-known pakicetid fossils are from Early Eocene strata in Pakistan, and they are regarded as the most primitive members of the Order Cetacea (Thewissen and Hussain, 1998; Thewissen et al., 2001, 2009; Gingerich, 2005; Uhen, 2010). Three genera have been placed in the Pakicetidae: *Ichthyolestes*, *Pakicetus* and *Nalacetus*. The first named pakicetid is *Ichthyolestes pinfoldi* (originally based on a left maxillary fragment preserving an M3 and incomplete M2) from the Middle Eocene Kuldana Formation of the lower Chharat Series at the locality 21 in Ganda Kas north of Basal in northwestern Pakistan (Dehm and zu Oettingen-Spielberg, 1958; Szalay and Gould, 1966). As its name suggests, when Dehm and Oettingen-Spielberg first described those fossils, they did not think that the specimens had any relationships with whales. Instead, they believed that *Ichthyolestes* is a mesonychid (Dehm and zu Oettingen-Spielberg, 1958). West (1980) followed the suggestion of Gingerich (1977) and assigned *Ichthyolestes* to the Protocetidae, setting a kind of connection with the origin of whales. One year later, Gingerich and Russell (1981) formally assigned *Ichthyolestes* to Cetacea, and established another pakicetid genus – *Pakicetus*, based on a posterior portion of a skull, a lower jaw fragment preserving p2-p4 and some isolated teeth, which were discovered from the late Early or early Middle Eocene Kuldana Formation near the Chorlakk Village in the Kohat District in northwestern Pakistan. Thewissen et al. (2001) reported two partial skeletons of *Ichthyolestes* and *Pakicetus*, setting the model for the most basal walking whales and elucidating the relationships between these two taxa and relationships of them to other mammals. The last genus included in Pakicetidae is *Nalacetus*. The only known species of the genus, *Nalacetus ratimitus*, is represented by two maxillary fragments and a lower jaw fragment discovered from the Early Eocene redbeds of the lower Kuldana Formation in northern Pakistan (Thewissen and Hussain, 1998).

Although many recent phylogenetic analyses support the hypothesis that pakicetids are the most basal members of Cetacea, there are actually very few synapomorphies shared by pakicetids and other whales. The synapomorphies include the narrow and elongated snout and cheek, incisors and canines in line with the cheek teeth, presence of buccolingually compressed premolars, a tympanic involucrum, and pachyosteosclerosis in the postcranial bones (Luo and Gingerich, 1999; Thewissen et al., 2001, 2007, 2009; Uhen, 2010). Besides these features, the general shape of pakicetids is more similar to that of mesonychid than to other mammals.

The body plan of pakicetids is very different from any crown whale, but quite typical

for a terrestrial mammal. They were small to medium sized mammals, no bigger than a wolf. Their tails are long, their limbs are slim, their astragali have the typical double trochleae of artiodactyls, and their toes were probably hoofed. The sacrum of pakicetids consists of four solidly fused vertebrae, and they possess a strong sacroiliac joint facet, a condition typical for all land mammals. Their ear region retains a functional external auditory meatus, a tympanic annulus for supporting the tympanic membrane, and a tympanic bulla closely attached to the mastoid process of petrosal, squamosal, and occipital. These characters all suggest that the ears of pakicetids were able to receive and transmit air-borne sound (Luo and Gingerich, 1999). High resolution CT scanning also reveals that the semicircular canals of the inner ear of *Ichthyolestes*, a smaller pakicetid than *Pakicetus*, are proportionally large, within the variation range of terrestrial mammals, and proportionally much larger than other extinct and extant whales (Spoor et al., 2002).

Pakicetids do have some features that probably were adaptive or exapted to life in the aquatic environment. In many aquatic mammals, limb bone cortices are thick, and their medullary cavities are relatively small. This modification is called pachyostosis, osteosclerosis, or pachyosteosclerosis. Pachyosteosclerosis in aquatic mammals makes their bones heavier (denser) compared to the bones of terrestrial mammals, reducing their buoyancy. Pakicetid postcranial bones show the pachyosteosclerotic condition. For instance, their medullary cavity comprises up to 57% of the total thickness of their femur, a proportion similar to extant hippopotamus but lower than most terrestrial mammals (Thewissen et al., 2007, 2009). The ear region of pakicetids possesses a tympanic involucrum, which is a condition referring to the thickening of the medial rim of the bulla. Luo and Gingerich (1999) suggested that presence of the tympanic involucrum is a result of the increase of the density of the bulla, similar to the same pachyosteosclerotic condition in their postcranial bones. Nummela et al. (2004) observed that the rostromedial side of the thickened tympanic is not fused with the petrosal in pakicetids. Therefore, the medial side of the tympanic forms a loosely suspended center of bony mass that could vibrate independently of the petrosal. That feature is an essential condition for enhanced transmission of bone-conducted sound in all whales.

All the pakicetid fossils were discovered from the fresh water sediments. If the pakicetids were indeed semi-aquatic, they must have been living close to fresh water environments, such as rivers or lakes. Studies on tooth isotopic values indicate that they were occupying a freshwater niche (Thewissen et al., 1996b; Roe et al., 1998; Clementz et al., 2006).

3.2 Ambulocetidae

The Family Ambulocetidae includes three genera: *Gandakasia*, *Himalayacetus* and *Ambulocetus* (Dehm and zu Oettingen-Spielberg, 1958; Gingerich and Russell, 1981; Thewissen et al., 1994, 2009). All ambulocetid fossils were collected in the near-shore shallow marine or costal deposits in the northern Pakistan and northwestern India. *Gandakasia potens* was the first-discovered species of this group, and was originally represented by a p4 fragment, a

dentary fragment with a partial m1 and complete m2, and an isolated complete m3 (Dehm and zu Oettingen-Spielberg, 1958; Szalay and Gould, 1966). Those specimens were uncovered at the locality 18 in the Early-Middle Eocene of the Kuldana Formation of the lower Chharat Series in Ganda Kas north of Basal in northwestern Pakistan (Dehm and zu Oettingen-Spielberg, 1958; Szalay and Gould, 1966). Just like *Ichthyolestes*, when *Gandakasia* was first described, Dehm and Oettingen-Spielberg suggested that it was a mesonychid (Dehm and zu Oettingen-Spielberg, 1958). Gingerich (1977) assigned an isolated lower molar collected in the early Middle Eocene Kohat Formation in the Kala Chitta mountains of the Punjab Province in Pakistan to *G. potens*, and suggested that *Gandakasia* is actually an archaeocete rather than a mesonychid. However, his postulation was not based on the anatomical characters, but the fact that the fossil bearing Kohat Formation is marine deposit with *Gandakasia* as the only-known mammal from that formation (Dehm and zu Oettingen-Spielberg, 1958; Gingerich, 1977). West (1980) formally assigned *Gandakasia* to the Family Protocetidae, based on some dental similarities shared by *Gandakasia* and protocetids. This taxonomic assignment was accepted by Gingerich and Russell (1990) in their later taxonomic framework for archaeocetes. However, Thewissen et al. (1996a) considered *Gandakasia* as more similar to *Ambulocetus* than to any protocetids, and therefore transferred *Gandakasia* to the Family Ambulocetidae. *Gandakasia* has smaller size and a trigonid lower than that of *Ambulocetus* (Thewissen et al., 1996a). Otherwise the two species are very similar to each other. The taxonomy assignment of *Gandakasia* to the Family Ambulocetidae is accepted by most later researchers (e.g. Cooper et al., 2009; Uhen, 2010). *Himalayacetus* was allocated originally in the Pakicetidae (Bajpai and Gingerich, 1998), but later researchers believe that its morphology and living environment are more consistent with those of ambulocetids (Thewissen and Williams, 2002; Thewissen et al., 2009).

The type species of the Family Ambulocetidae, *Ambulocetus natans*, is represented by a relatively complete skeleton, which is the source for the reconstruction of the anatomical characteristics of ambulocetids and for the diagnosis of the Family Ambulocetidae (Thewissen et al., 1994, 1996a, 2001). *Ambulocetus* was a kind of powerful and stout animal, about the same size as the extant walrus. The dental morphology of *Ambulocetus* closely resembles that of pakicetids, but *Ambulocetus* is much larger than any pakicetid, and the cranial and postcranial bones of *Ambulocetus* exhibit more features related to an aquatic life (Thewissen et al., 1994, 1996a, 2001). As in most Middle Eocene and all younger cetaceans, the orbit of *Ambulocetus* is positioned dorsally below the supra-orbital shield and facing laterally, and that is thought to be an adaptation, as in modern amphibious mammals (such as the hippopotamus), for submerged life (Thewissen et al., 1994, 1996a, 2001). The ectotympanic bulla of *Ambulocetus* is very large. The relative width of the bulla (width of the bulla relative to width of the skull at the level of the glenoid condyle) is over 20%, a feature shared with protocetids and basilosaurids (Luo and Gingerich, 1999). In crown odontocetes, the mandibular canal is enlarged and fat-filled, and this function to transmit underwater sound to the middle ear. The earliest record of this character is in *Ambulocetus* (Thewissen et al., 1994).

Ambulocetids must have been an amphibious mammal, able to move both on land and in the water. Their strong sacrum consists of four fused vertebrae with a well-developed sacroiliac joint facet as in typical land mammals (Thewissen et al., 1996a; Madar et al., 2002). On the other hand, the short but powerful limb bones of *Ambulocetus* are clearly pachyosteosclerotic (Thewissen et al., 2009). The olecranon of the ulna comprises almost one-fourth of the total ulna length, a feature that provides a strong lever for elbow extension and wrist flexion as in some aquatic mammals (Thewissen et al., 1994, 1996a; Madar et al., 2002). The feet of *Ambulocetus* are much larger than the hands. The relative lengths of the thighs, feet, and hands of *Ambulocetus* are similar to those of river otters (Thewissen and Fish, 1997). Combining its robust muscular tail, the animal must have been quite similar to otters who use their hind limb as the main propulsor (Thewissen and Fish, 1997; Thewissen et al., 2001; Madar et al., 2002).

An aquatic life for *Ambulocetus* is suggested by many anatomical specializations, and is also consistent with the stable isotope data (Roe et al., 1998). In life, *Ambulocetus* may have been an ambush hunter similar to a modern crocodile, and its external appearance may have looked just like a crocodile (Thewissen et al., 1996a).

Ambulocetid fossils have all been found in near-shore shallow marine or costal deposits (Dehm and zu Oettingen-Spielberg, 1958; Gingerich and Russell, 1981; Thewissen et al., 1994, 2009). In life, they may occupy coastal swamps or forests, probably near the mouth of a river (Roe et al., 1998). The osmoregulatory system of extant marine cetaceans are adapted the excess salty environment by ingesting seawater (Thewissen et al., 1996b). Thewissen et al. (1996b) determined the oxygen isotope composition of phosphate in the teeth of early cetaceans, and found that ambulocetids had not evolved the ability to ingest seawater, but instead had to depend on a freshwater source.

3.3 Remingtonocetidae

Remingtonocetidae is a diverse archaeocete group, including *Remingtonocetus*, *Attockicetus*, *Kutchicetus*, *Dalanistes*, and *Andrewsiphius* (Kumar and Sahni, 1986; Gingerich et al., 1995b, 2001b; Bajpai and Thewissen, 2000; Thewissen and Hussain, 2000; Gingerich, 2005; Thewissen and Bajpai, 2009; Thewissen et al., 2009). The type species of *Remingtonocetus* and the Family Remingtonocetidae, *R. harudiensis*, was originally assigned to *Protocetus* (Sahni and Mishra, 1975). Kumar and Sahni (1986) revised a series of specimens discovered in the Middle Eocene Chocolate Limestone of southwestern Kutch, India, and named the genus *Remingtonocetus* and the Family Remingtonocetidae.

Dalanistes from the Middle Eocene Domanda Formation of the Sulaiman Range, Pakistan is very similar to *Remingtonocetus*. It differs from *Remingtonocetus* by larger size and more robust premolars and molars (Gingerich et al., 1995b, 2001b).

The oldest and most primitive remingtonocetid is *Attockicetus praecursor*. The holotype and the only known specimen is a fragmentary skull discovered from a horizon near the contact between the Kuldana and Kohat formations of the Kala Chitta Hills in northern Pakistan

(Thewissen and Hussain, 2000). *Attockicetus* was identified as a remingtonocetid archaeocete based on its elongated snout, small and laterally-placed orbits, low and wide braincase, and oval-shaped tympanic bone (Thewissen and Hussain, 2000). It differs from other remingtonocetids in the presence of large protocones on the upper molars, and their relatively anteriorly positioned orbits (Thewissen and Hussain, 2000). The two characters suggest that *Attockicetus* is more primitive than other remingtonocetids (Thewissen and Hussain, 2000). Cooper et al. (2009) reported two lower premolars (p3 and p4) from the Kuldana Formation of the Kala Chitta Hills, and they tentatively assigned the two specimens to *Attockicetus*. If they are correct, it would imply that the earliest remingtonocetids may have been contemporaneous with pakicetids.

Andrewsiphius and *Kutchicetus* are two closely related taxa. Thewissen and Bajpai (2009) proposed a subfamily of Remingtonocetidae, Andrewsiphinae, for the two genera based on a number of synapomorphies, including the extremely slender jaw, fused mandibular symphysis, narrow palate and rostrum, and lower molars that have a low crown with three cusps lined up rostrocaudally. The two genera are represented by partially preserved skeletons, which are the major source of data for the reconstruction of the locomotory pattern of remingtonocetids. *Andrewsiphius* was described originally by Sahni and Mishra (1975) as an odontocete. Fordyce (1981) later suggested it was a protocetid. Kumar and Sahni (1986) then assigned it to the Remingtonocetidae. *Andrewsiphius* was discovered from a slightly younger horizon than that of *Remingtonocetus*. *Andrewsiphius* differs the almost contemporary *Remingtonocetus* and may be more derived than *Remingtonocetus* by possessing an extremely long mandibular symphysis that distally extends as far as the third molar (Kumar and Sahni, 1986). *Kutchicetus* was found in the Middle Eocene Harudi Formation of Kachchh, India (Bajpai and Thewissen, 2000), and is the smallest remingtonocetid. It differs from *Andrewsiphius* by having slender tail vertebrae and single-rooted anterior premolars (Thewissen et al., 2009).

The remingtonocetids retain many primitive features shared with pakicetids and ambulocetids, such as full complement of upper and lower teeth (dental formula 3.1.4.3/3.1.4.3), well developed upper third molars, large nasal bones, anteriorly positioned dorsal narial openings, and overhanging nasals, and they also possess many autapomorphies (Gingerich et al., 2001b; Kumar and Sahni, 1986). Remingtonocetids all have very elongated and narrow skull and mandible. The skulls have well-developed accessory air sinuses. The ear bones are partially isolated. Two mandibular halves are laterally compressed and appressed, with an extraordinarily long and usually unfused symphysis. The posterior border of the symphysis extends posteriorly beyond the premolar region. The teeth of remingtonocetids have crenulated cutting edges (Kumar and Sahni, 1986; Gingerich et al., 2001b; Thewissen and Bajpai, 2001, 2009; Gingerich, 2005; Thewissen et al., 2009).

As in ambulocetids, the postcranial bones of remingtonocetids suggest an amphibious life. They have relatively long cervical vertebrae. The sacrum composed of four fused vertebrae, suggesting powerful supports for the hind limbs. However, the acetabular notch in pelvis

of remingtonocetids is narrow to closed, and the femoral head lacks a distinct fovea. These features suggest that the hind limb of *Remingtonocetus* could not have been weight-bearing (Gingerich et al. 2001b). They may also suggest that the pelvic girdle of remingtonocetids probably was more flexible and capable of large amount of flexion and extension, as an adaption for swimming. The strong muscular and dorsoventrally compressed tail of remingtonocetids may have provided power during swimming, as in extant otters or beavers (Bajpai and Thewissen, 2000; Thewissen and Bajpai, 2009; Thewissen et al., 2009). No hand or foot bones of remingtonocetids are known. However, the solidly fused sacrum would have provided a strong base for hind limb, suggesting that foot of remingtonocetids may also have provided propulsion.

As in extant cetaceans, the semicircular canals of remingtonocetids are relatively small (Spoor et al., 2002). This character may indicate that remingtonocetids have evolved in the adaptive direction of modern cetacean balance organs, even though their body plan is far different from extant cetaceans.

The sound transmission mechanism in remingtonocetid shows a combination of features found in pakicetids and modern odontocetes (Nummela et al., 2004). Remingtonocetids have a large mandibular foramen, indicating the presence of mandibular fat pad. The contact between periotic and tympanic bones is loose, and the involucrum is not attached to the periotic but suspended. The tympanic membrane in remingtonocetids is probably in an elongated conical shape, an intermediate form between terrestrial mammals and modern cetaceans. The size and shape of the ear ossicles, and the relation between ossicular mass and tympanic plate area in remingtonocetids are similar to those in modern whales. All of these characters suggest that the auditory system of remingtonocetids had developed a sound transmission mechanism similar to modern cetaceans (Thewissen et al., 2009).

Remingtonocetid fossils have been collected in a variety of shallow marine or costal environments, including near-shore and lagoonal deposits (Gingerich et al., 1995b). Differing from ambulocetids, who relied on freshwater, analysis of stable oxygen isotopes suggests that most remingtonocetids were independent of freshwater (Roe et al., 1998). That means remingtonocetids were more adapted to marine life than ambulocetids.

3.4 Protocetidae

Protocetidae consists of the most diverse family of Archaeoceti. Nineteen genera have been described and assigned in Protocetidae (Table 1). Protocetids retain a full dental complement (dental formula 3.1.4.3/3.1.4.3). The eyes of protocetids are relatively large and laterally placed. The interorbital distance is large. A thick and flat supraorbital shield is always present. The nasal opening of protocetids is not at the tip of the snout, but located further posterior on the snout. These characters distinguish protocetids from all the other more basal cetaceans (Gingerich et al., 1995a, 2001a, b; Nummela et al., 2006; Thewissen et al., 2009).

Relatively well-preserved postcranial fossils are known in *Rodhocetus* and *Artiocetus*

from Pakistan (Gingerich et al., 1994, 2001a, b), and *Georgiacetus* from North America (Hulbert, 1998; Hulbert et al., 1998). The cervical vertebrae of protocetids are intermediate in length between those of remingtonocetids and basilosaurids (Gingerich et al., 2001b). Some protocetids, such as *Rodhocetus*, have a partially fused sacrum (Gingerich et al., 1994, 2001b). Other protocetids, such as *Georgiacetus*, lacks a fused sacrum (Hulbert, 1998; Hulbert et al., 1998). The first sacral of protocetids has a well-developed auricular processes, the acetabular notch in pelvis is open, and the femoral head generally has a distinct fovea (Gingerich et al., 2001b). In *Artiocetus* and *Rodhocetus*, the limbs are short, and the foot is much larger than the hand, a situation similar to *Ambulocetus* (Gingerich et al., 2001a; Thewissen et al., 2009).

As in remingtonocetids, the semicircular canals of protocetids are relatively small (Spoor et al., 2002). The sound transmission mechanism of the auditory system of protocetids is also similar to that of remingtonocetids, showing a combination of features of pakicetids and modern odontocetes (Nummela et al., 2004).

The skull shape, particularly the length and width of the snout, shows high diversity in protocetids. The differences probably reflect the diversity of foraging specializations in the group (Gingerich et al., 2001b). In the Asian *Artiocetus* and *Rodhocetus*, the relatively well-developed sacrum suggests that these animals were able to move on land, while in the North American *Georgiacetus*, the absence of a fused sacrum suggests that the limbs could not support the animal's weight. Therefore, some protocetids, such as *Georgiacetus*, may have been significantly more aquatic than the other protocetids (Hulbert, 1998; Hulbert et al., 1998; Gingerich et al., 2001a; Thewissen et al., 2009).

Protocetids are the first cetacean group with a global distribution. Fossils of them have been found in the Middle Eocene (49-40 Ma) of low latitude near-shore marine deposits in Asia, Africa, Europe, North America, and South America (Gingerich et al., 1997, 2001a, b; Williams, 1998; Geisler et al., 2005; Gingerich, 2007; Thewissen et al., 2009; Uhen, 2010; Uhen et al., 2011).

3.5 Basilosauridae

Basilosauridae is an archaeocete family that closely resembles the extant cetaceans (Uhen, 1998, 2004, 2010). Basilosauridae is also quite diverse with thirteen described genera (Table 1).

Similar to other archaeocetes but different from crown cetaceans, basilosaurids retain a heterodont dentition, with clear morphological differences between incisors, canines, premolars, and molars. The upper molars lack the M3. The premolars and molars have denticles. The nasal opening has shifted far backward to form the blowhole. The cervical vertebrae are very short. No distinct sacral vertebra is present. The pelvis lacks the ilium and does not articulate with the vertebrae. The hind limb is very reduced. The fore limbs are flippers, and the end of the tail had a fluke (Uhen, 2004, 2010; Thewissen et al., 2009).

In pakicetids, ambulocetids, and protocetids, the anterior part of the ectotympanic bulla has a broad articulation with the squamosal, but in mysticetes and odontocetes, the

articulation between ectotympanic and squamosal is totally absent (Luo and Gingerich, 1999). In basilosaurids, the contact between ectotympanic and squamosal is reduced to a narrow crest, showing a transitional state between the archaeocetes and crown cetaceans (Luo and Gingerich, 1999). The air-filled sinuses in the petrotympanic complex are much better developed in basilosaurids than in other archaeocetes. These characters suggest that basilosaurids probably had an ability for directional hearing, but less accurate than that in modern mysticetes. There is no evidence in their ear region that indicates a capability for high frequency hearing or echolocation (Luo and Gingerich, 1999).

Basilosaurids are the first fully aquatic cetaceans, and the most derived archaeocetes (as the sister group to the crown). They occurred from the late Middle Eocene through Late Eocene in Asia, Africa, Europe, New Zealand, and North America (Kellogg, 1936; Gingerich, 1992, 2007; Gingerich et al., 1997; Köhler and Fordyce, 1997; Uhen, 1998, 2004, 2010).

4 Phylogenetic relationship between cetaceans and other mammals

Osseous, soft tissue characters, and reproductive behavior all suggest that cetaceans are placental mammals. However, there are very few anatomical features that could link extant cetaceans with other placental mammals. Given their strong specialization and adaptation to aquatic life, and the lack of obvious extant transitional forms, the ancestry of the whales and their relationships to terrestrial mammals, as reflected from their systematic position in various classification systems, have long been a topic of debate. Relevant discussions can be traced back long before the pre-Darwinian era. In his classic monograph “The Orders of Mammals”, Gregory (1910) gave a detailed review on various hypotheses published before his work. From his review (Gregory, 1910), it is interesting to note that the modern prevalent hypotheses of the phylogenetic relationships between cetaceans and other mammals all have a long history.

4.1 Mesonychids

In 19th century, the prevalent idea was that cetaceans and sirenians were closely related, and in many classification systems, these two distinct mammalian groups were placed in the same order (Gregory, 1910). Except sirenians, the most widely accepted kin of cetaceans at that time were carnivores (Gregory, 1910). In the 1st edition of the “On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life”, Darwin suggested that whales may originate from a kind of hypothetical swimming bear: “I can see no difficulty in a race of bears being rendered, by natural selection, more and more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale” (Darwin, 1859, the “Origin”, 1st edition:184). From the 2nd to the 5th edition of the “Origin”, Darwin removed the swimming-bear origin hypothesis, and in the 6th edition of the book, he adopted Huxley’s hypothesis by regarding *Basilosaurus* and *Squalodon* as “connecting links with the aquatic carnivora” (Darwin, 1872, the “Origin”, 6th edition:302).

Van Valen (1966) was the first to suggest that cetaceans arose from mesonychids. His “evidences” were largely based on comparisons between *Protocetus* and mesonychids, and between *Protocetus* and hyaenodontids (Van Valen, 1966). Given the long-lasting hypothesis of the carnivore related origin of cetaceans, Van Valen’s (1966) proposal for a mesonychid origin hypothesis was not unexpected.

Mesonychids are a group of fossil mammals usually grouped as the Family Mesonychidae, and they were carnivorous animals of various sizes. Their dentition is superficially similar to those of true carnivorans, their skulls are also carnivoran-like in the presence of a high sagittal crest, a narrow brain case, and flaring zygomatic arches (Szalay and Gould, 1966; Van Valen, 1966). Traditionally mesonychids were referred to the Order Creodonta or Carnivora (Gregory, 1910; Simpson, 1945). Since late 1960s, researchers began to realize that mesonychids were very different from the true carnivorans (Szalay and Gould, 1966; Van Valen, 1966). They probably had hooves on all their toes, a feature similar to ungulates but not seen in creodonts or carnivorans (Szalay and Gould, 1966; Van Valen, 1966). Mesonychids also have an astragalus quite similar to that of artiodactyls (Van Valen, 1966). Van Valen (1966) formally transferred mesonychids to the Order Condylarthra, a polyphyletic taxonomic mess that includes many unrelated groups. Some later researchers placed mesonychids in their own order: Order Mesonychia (e.g. Gunnell and Gingerich, 1996; O’Leary, 2010). In spite of this, it is almost universally accepted that mesonychids were carnivorous.

Although Van Valen’s (1966) hypothesis was quickly accepted, solid evidence supporting this idea only came much later. The discovery of *Pakicetus* really strengthened the mesonychid-origin hypothesis (Gingerich et al., 1983). The dentation of *Pakicetus* closely resembles the carnivorous mesonychids and the Middle Eocene cetaceans. Thewissen et al. (1994) found that the dentation of *Ambulocetus* has weakly developed crest, similar to that of mesonychids. The toes of *Ambulocetus* are terminated by short phalanx that carried a convex hoof, a situation that is also shared with mesonychids. Zhou et al. (1995) studied the skull of *Sinonyx jiashanensis*, the most complete cranial specimen of any mesonychid. They found that some cranial characters, such as a short basicranium and absence of a postglenoid foramen, support a close relationship between cetaceans and mesonychids. Luo and Gingerich (1999) did an extensive survey on the basicranial morphology of mesonychids and archaeocetes. They compared 64 basicranial characters across various taxa in detail and concluded that mesonychids and cetaceans are sister groups.

A close phylogenetic relationships between mesonychids and cetaceans is supported by many cladistic analyses. In their pioneer cladistic analysis of the ungulate phylogeny, Prothero et al. (1988) showed that *Andrewsarchus* is the sister group of cetaceans, and placed mesonychids (excluding *Dissacus* and *Hapalodectes*) as the sister group of *Andrewsarchus* and cetaceans. Luo and Gingerich’s (1999) phylogenetic analysis based on their investigation of the basicranial morphology of mesonychids, cetaceans, artiodactyls, and other ungulates demonstrated that mesonychids and cetaceans form a monophyletic group with artiodactyls as

its sister group. A similar result was produced by O'Leary and Geisler (1999). They presented a detailed phylogenetic analysis based on a data matrix including 123 morphological characters scored for 40 taxa, the largest in terms of the number of taxa and characters. The most parsimonious tree of O'Leary and Geisler (1999) indicated that Mesonychidae and Cetacea form a monophyletic group, and Artiodactyla forms another monophyletic group that is the sister of Mesonychidae + Cetacea.

4.2 Artiodactyls

The idea of a close artiodactyl-cetacean phylogenetic relationship can also be traced back into the pre-Darwinian era, although it was not as prevalent as the carnivore-origin hypothesis. In 19th century, some researchers or scholars have noticed that visceral organs of the cetaceans far more resembling those ungulates than the carnivorans. Flower (1883a, b, c, d) is probably the first person who formally proposed that cetaceans originated from ungulates (particularly artiodactyl ungulates). He even pointed out that the skull of *Basilosaurus* resembled that of a primitive pig-like ungulate than that of a seal. It is not hard to speculate that this pig-like ungulate is probably *Entelodon* (the genus was established in 1846).

Gregory (1910) suggested that cetaceans derived from some insectivore-creodont ancestor. He (Gregory, 1910:467-468, figs. 31, 32) depicted an evolutionary diagram that showed cetaceans, artiodactyls, carnivores, creodonts, and mesonychids all arising from the same stock. Cetaceans derived first, then mesonychids and artiodactyls formed an offshoot. Diverse carnivores derived even later. Perissodactyls and other ungulates belonged to a different stock. If we translate this relationship into modern cladogram, it will be: (((mesonychids, artiodactyls), carnivores), cetaceans), perissodactyls and other ungulates). This phylogenetic framework is not very different from the modern hypothesis. However, Gregory's (1910) hypothesis was largely ignored by later scholars. Only the insectivore-creodont origin of cetaceans was quoted occasionally, but always out of context.

Mossman (1937, 1987) placed cetaceans and artiodactyls together as derivatives of a primitive ungulate stock based on the similarities in the structure of the fetal membranes and accessory uterine structures. The later stages of the fetal membranes of artiodactyls all undergo comparable blastocyst elongation. The only non-artiodactyl group that shows evidence of this elongation is Cetacea (Mossman, 1937, 1987; Stump et al., 1960).

Boyden and Gemeroy (1950) used serological methods to investigate the interordinal relationship of cetaceans to 13 orders of mammals. Their precipitin tests showed that the interordinal reaction (as determined by the quantitative photoelectric technique) between cetaceans and artiodactyls is much higher than values between cetaceans and other tested mammals. The result suggested that the serum proteins of representative cetaceans and artiodactyls are much more similar than those between cetaceans and other tested mammals, implying a closer systematic relationship between cetaceans and artiodactyls.

Goldstone and Smith (1966) analyzed the amino sequence of the heart cytochrome c of

the California gray whale (*Rhachiancetes glaucus*), and found it most closely resembles those of bovine, porcine, and ovine heart tissues, differing from those latter in only two residues. They suggested that their finding is consistent with the view that cetaceans derive from an ancestor close to artiodactyls.

Goodman et al. (1985) carried on pioneer work in the application of the parsimony method on protein amino acid and DNA nucleotide sequence data. Their results provided fresh evidences on cladistic branching patterns at various taxonomic levels of mammals. They (Goodman et al., 1985) found that cetaceans and artiodactyls are closely related and form a clade, a result similar to those obtained by Boyden and Gemeroy (1950), and Goldstone and Smith (1966) decades before. The work of Goodman et al. (1985) was published when molecular systematics began to thrive. Numerous studies based on amino acid, DNA, and RNA sequences followed their steps and overwhelmingly supported the cetacean-artiodactyl relationship (e.g. Irwin and Arnason, 1994; Gatesy et al., 1996; Montgelard et al., 1997; Murphy et al., 2001a, b; Arnason et al., 2002, 2004; Arnason and Janke, 2002; Springer et al., 2003, 2007). Montgelard et al. (1997) first defined the superordinal name “Cetartiodactyla” for the monophyletic clade Cetacea + Artiodactyla.

Paleontological data that supported an artiodactyl-cetacean relationship came much later. Gingerich et al. (1990) reported the hind limb fossil of Middle Eocene *Basilosaurus isis* from Egypt. This discovery showed for the first time that the third and fourth metatarsals of this archaeocete are the longest and largest metatarsals, a condition termed as paraxonic pes (Gingerich et al., 1990). Although it is widely cited that the paraxonic foot of *Basilosaurus* supports a close affinity to artiodactyls, both artiodactyls and mesonychids have a paraxonic foot. Gingerich et al. (1990) seem to suggest that the paraxonic foot of *Basilosaurus* is consistent with the derivation of cetaceans from mesonychids. Thewissen and Hussain (1993) reported an isolated left incus, which was assigned to *Pakicetus*. The tiny bone has a moderately long crus breve, short crus longum, partly inflated incudal body, and partly rotated joint facets for malleus. Thewissen and Hussain (1993) suggested that this morphology is intermediate between artiodactyls and typical cetaceans. Maas and Thewissen (1995) examined the microstructure of the tooth enamel of *Pakicetus*, *Diacodexis* (the earliest artiodactyl), and a mesonychid. Their results showed that the enamel organization of *Pakicetus* is similar to both *Diacodexis* and the mesonychid. They suggested that artiodactyls, mesonychids, and cetaceans are all closely related.

The ankle bones of archaeocetes played a critical role for setting the phylogenetic links between cetaceans and ungulates (Thewissen et al., 1998; Thewissen and Madar, 1999). Thewissen et al. (2001) reported two partial skeletons of two pakicetids, which include the astragali that have characteristics clearly diagnostic for Artiodactyla. Almost simultaneously (one day later on the journal cover), Gingerich et al. (2001a) reported two partial skeletons of two protocetids, that also preserve the astragali. Like artiodactyls, the heads of the astragali of these archaeocetes have a well-developed navicular trochlea. The sustentacular

facet is elongated and forms a hinge that rotates dorso-plantarly. The ectal facet is a small oval concavity and laterally placed. These discoveries are very important for clarifying that cetaceans evolved from early artiodactyls rather than from mesonychids.

Thewissen and colleagues suggested that the mesonychid-cetacean hypothesis and the artiodactyl-cetacean hypothesis were not mutually exclusive (Thewissen et al., 1998). There is still the possibility that mesonychids were the sister group of cetaceans, and both fell in the Cetartiodactyla. The phylogenetic analyses of O'Leary and colleagues suggested that it took only two steps longer than the shortest trees when mesonychids fell inside Artiodactyla and displaced *Indohyus* from a position close to Cetacea (O'Leary and Gatesy, 2008; Spaulding et al., 2009).

Morphologically the Order Artiodactyla is a very well diagnosed monophyletic group. Traditional classification usually divides it into three suborders: Tylopoda, Suiformes, and Ruminantia. The species of hippopotamus belong to a family of its own within the Suborder Suiformes.

Molecular phylogenetics not only indicates a close relationship between cetaceans and artiodactyls, but also overturns the monophyly of Artiodactyla. Most of the recent molecular phylogenies place hippopotami as the sister group of cetaceans, to the exclusion of other suiforms.

Irwin and Arnason (1994) first suggested that the hippopotamus is most closely related to the cetaceans, based on an extensive comparison of the DNA sequences of the mitochondrial cytochrome *b* gene of 28 species, representing 22 families and 10 orders. Graur and Higgins (1994) is sometimes cited as the first paper that proposed the hippopotamus-cetacean relationship. This paper (Graur and Higgins, 1994) independently (but two months later) found that cetaceans nested in the traditional Artiodactyla. Their (Graur and Higgins, 1994) analysis included 5 mitochondrial DNA sequences and 11 nuclear genes, but their taxon sampling was very limited. Hippopotamus actually was not included. Almost all later phylogenetic studies based on mitochondrial or nuclear genes or genomes support the sister relationship between hippopotamus and cetaceans (e.g. Gatesy et al., 1996; Gatesy, 1997; Murphy et al., 2001a, b; Arnason et al., 2002, 2004; Arnason and Janke, 2002; Springer et al., 2003, 2007).

Short interspersed element (SINE) and long interspersed element (LINE) are retroposons, a type of mobile genetic elements that have been amplified and integrated into a host genome by retroposition (process of integration of a reverse-transcribed copy of an RNA fragment). The integration of a SINE or LINE at a new locus is regarded as an irreversible event (Nikaido et al., 1999). This feature of SINEs and LINEs makes them excellent tools for reconstructing the phylogenetic relationships. A phylogenetic analysis based on 20 informative SINE/LINE retropositional events indicates that hippopotamus and cetaceans form a monophyletic group, excluding other suiforms (Nikaido et al., 1999).

Geisler and colleagues (Geisler and Uhen, 2003; Geisler and Theodor, 2009) believe that molecular and morphological evidence for the phylogeny of cetaceans, hippopotamus,

and other artiodactyls are congruent. Morphological data supports placement of cetaceans within the Artiodactyla, and hippopotamus as the closest relatives of cetaceans (Geisler and Uhen, 2003; Geisler and Theodor, 2009). The analyses of Boisserie et al. (2005) based on morphological data also support a close affinity between hippopotamus and cetaceans. However, their (Boisserie et al., 2005) analysis included artiodactyls and cetaceans only, and assumed a priori monophyly of artiodactyls and cetaceans.

5 Controversy and future work

Although phylogenetic analyses based on molecules overwhelmingly suggest a close relationship between artiodactyls (particularly hippopotamus) and cetaceans, analyses of the most recent update of the data matrix including fossils and morphological data continually support the sister-group relationship between mesonychids and cetaceans, when the positions of extant mammals were not constrained by a massive amount of molecular characters (O’Leary and Gatesy, 2008; Spaulding et al., 2009).

Morphology based phylogenetic analyses have not arrived at a consensus on the hippopotamus-cetacean relationship either. Analyses of Geisler and colleagues (Geisler and Uhen, 2003; Geisler and Theodor, 2009), and Boisserie et al. (2005) suggest hippopotamus as the closest relative of cetaceans. A few other analyses based on large morphological data matrices all failed to support the hippopotamus-cetacean sister relationship, if extant taxa were not constrained with molecular data (Thewissen et al., 2007; O’Leary and Gatesy, 2008; Spaulding et al., 2009).

A sister relationship between hippopotamus and cetaceans would imply that there are some early Paleogene fossils that would fill the morphological gap between hippopotamus and cetaceans. During the past few decades, discoveries of stem cetaceans demonstrate the transition of the cetacean ancestor from a typical terrestrial runner to a derived fully aquatic dweller. However, these stem cetaceans do not exhibit many convincing morphological characters linking them to hippopotamus. Instead, these stem cetaceans show many features resembling those in mesonychids.

Thewissen et al. (2007, 2009) suggested that the Eocene south Asian artiodactyl raoellids (*Indohyus* and *Khirtharia*) are the sister group of cetaceans. The raoellid *Indohyus* resembles cetaceans, and is unlike other artiodactyls in the structure of its ears and premolars, in the density of its limb bones, and in the stable-oxygen-isotope composition of its teeth (Thewissen et al., 2007, 2009). These characters seem have provided quite solid evidence for the hypothesis of artiodactyl-origin of cetaceans, but they make the link between hippopotamus and cetaceans even more unlikely, although manipulating the data can sometime place hippopotamus, raoellids, and cetaceans in the same clade (e.g. Geisler and Theodor, 2009).

The fossils of Hippopotamidae provide little help for the discussion on the hippopotamus-cetacean relationship. Early hippopotamid fossils are all from Africa, and no earlier than the

Early Miocene (Pickford, 1983, 1998, 2007). It has long been suggested that hippopotamids were related to the Eocene anthracotheriid artiodactyls and not to cetaceans (Gaziry, 1987; Gentry and Hooker, 1988; Weston, 2000). A long ghost lineage still exists between the supposed anthracotheriid ancestor and the earliest hippopotamid fossils.

Most recent phylogenetic analyses suggest that anthracotheriids are closely related to hippopotamus and cetaceans, usually as the stem of the hippopotamus-cetacean clade (Boisserie et al., 2005, 2010; Thewissen et al., 2007; Geisler and Theodor, 2009; Spaulding et al., 2009; Orliac et al., 2010). Although anthracotheriid fossils are quite common, a detailed review of this group within the artiodactyl-cetacean context has not been done. Such work will certainly help to clarify the uncertain relationships close to and possible within the hippopotamus-cetacean clade.

Some of these phylogenetic analyses suggest that entelodontids are also closely related to hippopotamus and cetaceans. Entelodontids are either the sister group of hippopotamids or form the stem of the hippopotamus-cetacean clade (O'Leary and Gatesy, 2008; Spaulding et al., 2009). Entelodontidae is generally placed in the Suiformes. As with the anthracotheriids, it is also necessary and important to carry out a detailed review on entelodontids in a broad artiodactyl-cetacean related framework, and to incorporate more entelodontids in phylogenetic analyses.

Lacking transitional fossils is a platitude, but it is a plain fact that current available fossils still are not enough for setting a reliable phylogenetic framework between cetaceans and other mammals.

6 Conclusions

(1) Archaeocetes consist of a very diverse paraphyletic group.

(2) Pakicetidae, Ambulocetidae, Remingtonocetidae, Protocetidae, and Basilosauridae show a gradual transformation from a mainly terrestrial animal to fully aquatic animal.

(3) Molecular phylogenetic analyses support a close artiodactyl-cetacean relationship. Paleontological and morphological data also provide convincing evidence for reconstructing such a relationship.

(4) Phylogenetic analyses based on paleontological and morphological data still support a broad mesonychid-cetacean relationship, if the positions of extant cetaceans and artiodactyls are not constrained by molecular data.

(5) Recent molecular phylogenetic analyses support a close hippopotamus-cetacean relationship, but do not support the monophyly of Artiodactyla.

(6) Paleontological and morphological data for the hippopotamus-cetacean relationship are not without problems.

(7) Detailed review and more extensive phylogenetic analyses on anthracotheriids and entelodontids likely will clarify the artiodactyl-cetacean relationship, and particularly the hippopotamus-cetacean relationship.

Acknowledgements We thank Dr. Thomas Stidham for his assistance in refining the English text. We thank Dr. Thomas Stidham and Li Lu-Zhou for their valuable comments that improved the manuscript. We are grateful for the instructive suggestions from Drs. Wang Yuan-Qing and Zhang Zhao-Qun. This project was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (CAS, XDB03020501), the National Basic Research Program of China (2012CB821904), and the CAS 100-talent Program.

基干鲸类的多样性及其与中兽和偶蹄类的系统关系

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摘要: 在鲸类的演化历史中, 由陆生动物转化成完全的水生动物的过程是一个由来已久的演化谜题。基干鲸类的多样性很高, 化石记录也很完整。5个科一级的基干鲸类演化支系组成一个并系类群, 包括: 巴基鲸科(Pakicetidae)、游走鲸科(Ambulocetidae)、雷明顿鲸科(Remingtonocetidae)、原鲸科(Protocetidae)和龙王鲸科(Basilosauridae)。最基干的鲸类巴基鲸科动物可能是一种半水生动物, 生活在接近淡水的环境中, 代表了陆生偶蹄类向水生鲸类演化的初始一步。更为进步的游走鲸类具有更多适应于水生生活的特征, 而且可能更加适应于海水环境。雷明顿鲸类的平衡觉器官和声音传导机制已经表现出向现代鲸类方向演化的趋势。基于稳定氧同位素分析的研究表明, 雷明顿鲸类可能完全是海生的。原鲸类的多样性非常高, 是鲸类中最先实现全球分布的类群。原鲸保留有发育良好的后肢, 但是它们的髌骶关节很松甚至消失。龙王鲸类是鲸类冠类群的绝灭姊妹群。鲸类与其他哺乳动物的系统关系一直存在争议, 分子生物学、古生物学和形态学证据都支持鲸类与偶蹄类的亲缘关系较近, 但是流行的河马—鲸类亲缘假说尚缺乏坚实的古生物学和形态学数据支持。对石炭兽类和犛类开展详细的系统分析和研究, 将有助于厘清河马—鲸类亲缘假说中的不确定关系。如果不使用分子数据来限定现代鲸类和偶蹄类的系统位置, 仅使用古生物学和形态学数据的分析仍然支持传统的中兽—鲸类亲缘假说。

关键词: 古鲸亚目, 偶蹄目, 中兽科, 河马, 系统发育

中图法分类号: Q915.875, Q915.876 **文献标识码:** A **文章编号:** 1000-3118(2015)02-0153-24

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