The triple origin of whales

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ABSTRACT—Workers presume the traditional whale clade, Cetacea, is monophyletic when they support a hypothesis of relationships for baleen whales (Mysticeti) rooted on stem members of the toothed whale clade (Odontoceti). Here a wider gamut phylogenetic analysis recovers Archaeoceti + Odontoceti far apart from Mysticeti and right whales apart from other mysticetes. The three whale clades had semi-aquatic ancestors with four limbs. The clade Odontoceti arises from a lineage that includes archaeocetids, pakicetids, tenrecs, elephant shrews and anagalids: all predators. The clade Mysticeti arises from a lineage that includes desmostylians, anthracobunids, cambaytheres, hippos and mesonychids: none predators. Right whales are derived from a sister to *Desmostylus*. Other mysticetes arise from a sister to the RBCM specimen attributed to *Behemotops*. Basal mysticetes include *Caperea* (for right whales) and *Miocaperea* (for all other mysticetes). Cetotheres are not related to aetiocetids. Whales and hippos are not related to artiodactyls. Rather the artiodactyl-type ankle found in basal archaeocetes is also found in the tenrec/odontocete clade. Former mesonychids, *Sinonyx* and *Andrewsarchus*, nest close to tenrecs. These are novel observations and hypotheses of mammal interrelationships based on morphology and a wide gamut taxon list that includes relevant taxa that prior studies ignored. Here some taxa are tested together for the first time, so they nest together for the first time.

INTRODUCTION

Marx and Fordyce (2015) reported the genesis of the baleen whale clade (Mysticeti) extended back to *Zygorhiza, Physeter* and other toothed whales (Archaeoceti + Odontoceti). Earlier Fitzgerald (2006) and Fordyce and Marx (2016) discussed 'basal mysticetes' with teeth. Even earlier Emlong (1966) described the newly discovered *Aetiocetus*, "If it were not for the presence of functional teeth on this mature specimen, this cetacean could easily be placed in the suborder Mysticeti." Marx et al. (2016) proposed a scenario in which "the transition from raptorial to baleen-assisted filter feeding was mediated by suction, thereby avoiding the problem of functional interference between teeth and the baleen rack." Lambert et al. (2017) echoed this conjecture in their description of toothy *Mystacodon*, a taxon they considered the earliest known member of the Mysticeti. Thewissen (1994), Thewissen et al. (2007), and Thewissen et al. (2009) supported the traditional view that "whales with legs", like *Maiacetus*, were basal to all hydropedal whales. Unfortunately, these studies did not include elephant shrews, tenrecs, anthracobunids and desmostylians, taxa omitted from, but relevant to phylogenetic studies of whales according to the present analysis (Fig. 1).

The monophyly of the traditional clade, Cetacea, has been challenged only rarely. Kükenthal (1891) concluded, "We are justified in maintaining that the toothed whales are of much earlier origin than whalebone whales, and that the terrestrial ancestors of the two divisions were not identical." Miller (1923), Yablokov (1965) and Zhemkova (1965) thought odontocetes and mysticetes arose from different and unidentified ancestors. In 1968 Van Valen listed 20 traits that differ in odontocetes and mysticetes, but considered cetaceans monophyletic and toothed *Aetiocetus* a mysticete. This has remained the traditional view to the present day.

Here the taxon list of whale ancestors is expanded to include untested candidates. The results of this wide-gamut, online phylogenetic analysis, commonly known as the large reptile tree (= LRT; www.ReptileEvolution.com/reptile-tree.htm; subset in Fig. 1), challenge the monophyly of the traditional clade 'Cetacea.' The LRT includes 1165 tetrapod taxa. With this wider gamut of taxa the two universally recognized clades of whales, Odontoceti and Mysticeti, arise in parallel from distinct terrestrial mammal clades (Fig. 1). Members of the Odontoceti are derived from aquatic archaeocetids, pakicetids, tenrecs, terrestrial elephant shrews and anagalids in order of increasing distance. Members of the Mysticeti are derived from aquatic desmostylians (Fig. 3), anthracobunids, cambaytheres, hippos and terrestrial mesonychids. Right whales arise from different desmostylians than other mysticetes do. This novel hypothesis of interrelationships is well supported by fossils and extant taxa that document a gradual accumulation of odontocete and mysticete traits in separate but convergent lineages. This finds analogy in sirenians they also converge on whales in the loss of hind limbs and the development of tail flukes. Purported transitional taxa, *Aetiocetus* (Emlong, 1966) and *Mystacodon* (Lambert et al., 2017), nest with odontocetes, far from mysticetes in the LRT. *Janjucetus* and *Mammalodon* nest with *Anthracobune* in the lineage of desmostylians and mysticetes, far from odontocetes. Cetotheres were considered basal mysticetes (Lambert et al. 2017) due to their resemblance to aetiocetids. Here the small mysticetes, *Caperea* and *Miocaperea*, nest as basal mysticetes based on traits shared with desmostylians.

DNA studies do not include older fossils. Frequently molecular studies recover family tree topologies that do not match those of morphological studies (Fordyce and de Muizon, 2001). Molecular studies do not provide a gradual accumulation of physical traits in order to check that evolutionary changes are indeed tenable.

The evolutionary history of cetacean swimming from cursorial mesonychids promoted by Thewissen and Fish (1997) used the dorsoventral undulation of otters as a living analog for unknown transitional taxa. They assumed a monophyletic Cetacea and made no reference to tenrecs or desmostylians. They also expressed some concern in the transition from a cursorial mesonychid to a hydropedal whale, ironically without invoking the cursorial and aquatic hippo. Fordyce and de Muizon (2001) discussed similar issues without an adequate phylogenetic framework.

The problem with all prior studies has been taxon exclusion. No prior studies correctly identified the ancestors of pakicetids and mysticetes. Here all potential candidates for whale ancestry are tested going back to Devonian tetrapods. Here the 3x convergent loss of hind limbs and acquisition of tail flukes in the three ‘whale’ clades is based on a phylogenetic framework with very short ghost lineages. The present study also reveals several overlooked transitional traits and vestiges.

MATERIALS AND METHODS

The key advancement provided by the present tree topology (Fig. 1) is taxon inclusion. Prior workers with first hand access to whale specimens omitted relevant taxa. Over 1150 candidates for mysticete and odontocete ancestry were tested here using published images for most of the data. Results indicate that the exclusion of relevant taxa is a greater problem than lacking first hand access. The present list of 1165 taxa minimizes bias and tradition in the process of selecting ingroup and outgroup taxa for smaller, more focused studies because all major and many minor tetrapod clades are tested here. That means that all derived clades, including every tested whale, have outgroups extending back to Late Devonian tetrapods.

No characters used in the LRT are specific to the clades that include whales and their proximal ancestors. Although some characters are similar to those from various prior analyses, the present list (see Supporting Data; DataDryad.org/xxxxx to be completed when the ms. is accepted) was largely built from scratch. Traits specific to turtles or pterosaurs would have been useless on whales and tree shrews and vice versa. Generalized characters were chosen or invented for their ability to lump and split clades and for their visibility in a majority of tetrapod taxa, many of which had never been tested together. Up to this point, the 231 multi-state character set has proven sufficient to lump and separate 1165 taxa, typically with high Bootstrap scores. In the past, certain workers considered 231 characters too small for the number of tested taxa—when the taxon list was a quarter of the size it is now. Others thought the characters themselves were less than optimally fashioned. Not all opinions can be accommodated given the constraints of a single lifetime. Complete resolution in the LRT tree and high Bootstrap scores falsify any blackwashing levied against the present character list. For all of its faults, real or imagined, the LRT continues to work well as more taxa are added every week. All taxon subsets of the LRT (e.g. Fig. 1) raise the character/taxon ratio. All taxa in the LRT are generic, specific or species-based. Chimaeras are not employed.

Taxa and characters were compiled in MacClade 4.08 (Maddison and Maddison, 1990), then imported into PAUP* 4.0b (Swofford, 2002) and analyzed using parsimony analysis with the heuristic search algorithm. All characters were treated as unordered and no character weighting was used. Bootstrap support figures were calculated for 100 replicates. The cladogram, character list and data matrix accompany the manuscript and will be available in permanent repository here: www.Treebase.org/ xxxxx and www.DataDryad.org/xxxxxx (to be completed when the ms. is accepted).

Abbreviations: mya = million years ago; IVPP = Institute of Vertebrate Paleontology, Peking; NMV = Museum Victoria, Melbourne, Australia; RBCM = Royal British Columbia Museum, Victoria, Canada; UHR = University of Hokkaido Registration, Sapporo, Japan.

RESULTS

The LRT nests all tested taxa in near-complete resolution (2 MPTs with loss of resolution at the incomplete fossil of *Maelestes*). High Bootstrap scores are typically recovered. The traditional clades, Odontoceti and Mysticeti, nest apart from one another (Fig. 1). Both odontocetes and mysticetes had limbed precursors. Right whales descend from different desmostylians than all other mysticetes do. The last common ancestor of all whales is a sister to the tiny tree shrew-like taxo, *Maelestes* (Late Cretaceous; Wible, et al., 2007a, b).

The tenrec/odontocete clade

In the LRT (subset Fig. 1) odontocetes are derived from a placental mammal clade that had its origin with tiny, formerly arboreal insectivores, like *Maelestes*. Rabbit-sized *Anagale* (early Oligocene; Simpson, 1931) and *Leptictis* (early Oligocene; Leidy, 1868; Rose, 2006) split off next followed by the long-legged elephant shrew, *Rhynchocyon* (extant). The other extant elephant shrew, *Macroscelides* nested elsewhere. Former mesonychids, wolf-sized *Sinonyx* (late Paleocene; Zhou et al., 1995) and giant *Andrewsarchus* (middle Eocene; Osborn, 1924), split off next, followed by the tenrec clade. *Mesonyx* and other mesonychids nested elsewhere (see below). Bajpai and Gingerich (1998) associated *Himalayacetus* (early Eocene;) with the lineage of toothed whales. It is known from an incomplete dentary comparable to that of *Sinonyx* and is not tested here.

In the LRT the tenrec clade includes *Hemicentetes* (extant) and *Tenrec* (extant, formerly *Centetes*, Fig. 2), plus cat-sized *Leptictidium* (Early Eocene; Tobien 1962) and *Indohyus* (Eocene; Rao, 1971). The shrew-like 'tenrecs', *Limnogale*, *Microgale*, *Micropotamogale* and *Potamogale*, nested elsewhere and apart from the hedgehog-like 'tenrec,' *Echinops*.

At succeeding nodes, wolf-sized *Pakicetus* (Eocene) was considered "one of the oldest whales known anywhere" (Gingerich and Russell, 1981) upon its discovery. Larger *Maiacetus* (Eocene, Gingerich, et al., 2009) was unable to locomote on land due to a much longer torso, hydropedal forelimbs and vestigial hind limbs. It had a more robust tail, yet retained a skull similar to that of *Tenrec* (Fig. 2). Larger still, *Mystacodon* (Late Eocene; Lambert et al., 2017) and *Zygorhiza* (Late Eocene; True, 1908) was more fully hydropedal based on its relatively smaller pelvis. *Aetiocetus* (Oligocene; Emlong, 1966), *Chonecetus* (Oligocene; Russell, 1968; = *Fucacia* Marx et al., 2015) and NMV P252567 (Oligocene, Marx et al., 2016) were originally considered basal to the clade Mysticeti due to their resemblance to cetotheres. With more taxa these three nest together between *Zygorhiza* and the two tested extant odontocetes, *Orcinus* and *Physeter*. Many dozen species of extant and extinct toothed whales are known and could have been added to this taxon list, but the focus here is on basal taxa with terrestrial traits.

The mesonychid/mysticete clade

In the LRT mysticetes are derived from a mammal clade that had its origin with terrestrial *Mesonyx* (Eocene; Cope, 1872; Van Valen, 1966), derived from Paleocene or older ungulates (see below and Fig. 1). Phylogenetically *Mesonyx* is followed by semi-terrestrial *Ocepeia* (Paleocene; Gheerbrant et al., 2001, 2014) and *Hippopotamus* (extant). The next split produced *Cambaytherium* (Eocene; Rose et al., 2014) and *Cornwallius* (Early Oligocene; Cornwall 1922; Hay 1923, Beatty 2006a, b). The next split produced *Anthracobune* (Eocene; Pilgrim, 1940), *Mammalodon* (late Oligocene; Pritchard, 1939) and *Janujucetus* (late Oligocene; Fitzgerald 2006) in a clade. The basal desmostylians followed. These include *Neoparadoxia* (Barnes 2013; Miocene), *Paleoparadoxia* (Miocene; Reinhart, 1959), *Desmostylus* (Oligocene; Marsh, 1888; Inuzuka, 2009; Uno and Kimura, 2004) and the RBCM.EH2007.008.0001 specimen attributed to *Behemotops* (Oligocene; Domning, Ray and McKenna, 1986; Beatty and Cockburn, 2015). The two tested right whales (*Eubalaena* and *Caperea*) nested with *Desmostylus*. The remaining mysticetes nested with the RBCM specimen attributed to *Behemotops*.

Regaining a monophyletic ‘Cetacea’

In order to attract members of the Mysticeti to the strongly convergent Odontoceti, only two mysticete outgroup taxa need to be removed: *Desmostylus* and the RBCM specimen attributed to *Behemotops*. When that happens the mysticetes nest with *Physeter* and *Orcinus*. Conversely, in order to attract extant members of the Odontoceti to the Mysticeti, four odontocete outgroup taxa need to be removed: *Zygorhiza* and the three aetiocetids. When that happens *Physeter* and *Orcinus* nest with the mysticetes leaving *Maiacetus* and *Mystacodon* nesting with the pakicetids and tenrecs.

Nomenclature

The traditional clades ‘Cetacea’ (Brisson, 1762) and ‘Cetartiodactylia’ are no longer monophyletic in the LRT. The traditional clade ‘Artiodactylia’ is found to be polyphyletic in the LRT—unless *Hippopotamus* and all whales are omitted. The traditional clade ‘Whippomorpha’ (Cetacea + Hippopotamidae; Waddell, Okada and Hasegawa, 1999) is no longer monophyletic in the LRT. The clade Neoceti (Odontoceti + Mysticeti, Uhen, 2008) is no longer monophyletic. The clade Pelagiceti (Basilosauridae + Neoceti, Uhen, 2008) is likewise no longer monophyletic.

The traditional clade Mesonychia is here expanded to include *Mesonyx*, *Sus*, their last common ancestor and all of their descendants. In the LRT that list includes hippos, desmostylians, mysticeti, artiodactyls, elephants, sirenians, chalichotheres and perissodactyls. These are all decendants of a sister to *Mesonyx.*

A more restricted new clade, Mesonyketos ("middle claw-sea monster"), is proposed to include *Mesonyx*, *Hippopotamus*, their last common ancestor and all of their descendants. That clade includes the Desmostylia and both mysticete clades (Fig. 1). The Desmostylia is no longer an extinct clade.

The clade Mysticeti (Cope, 1891) traditionally includes all baleen whales. In order to remain monophyletic it must also include tested members of the Desmostylia (Reinhart, 1959). This makes 'Desmostylia' a junior synonym for Mysticeti unless applied to just *Neoparadoxia* and *Paleoparadoxia*, among tested taxa.

A new clade Tenreketos ("tenrec-sea monster"; from French tanrec, from Malagasy tàndraka, plus Greek ketos) is proposed for *Maelestes*, *Tenrec*, their last common ancestor and all of its descendants. That clade includes the traditional clade Archaeoceti, which now includes the smaller clade Odontoceti.

A new clade, Edafosia ("ground" in Greek), is proposed for *Maelestes*, *Phenacodus*, their last common ancestor and all of its descendants. In the LRT this clade includes mammals that plesiomorphically became ground dwellers. Edafosia is the smallest clade that contains all 'whales.'

DISCUSSION

Tenreketos

Many fossil taxa document transitional phases in the evolution of so-called 'land whales' to hydropedal taxa (Thewissen et al., 2007, 2009). That lineage traditionally begins with *Pakicetus*, *Indohyus* and related taxa. Here the ancestors of *Pakicetus* and *Indohyus* are recovered for the first time, and they are not artiodactyls.

In the LRT, *Maelestes* (skull 2 cm long) nests at the base of the Tenreketos (Fig. 1). Similar in size and shape to extant tree shrews, *Maelestes* was originally (Wible et al. 2007a, b) allied with *Asioryctes* far outside of the Placentalia, but deep within the Eutheria in a cladogram with few taxa in common with the LRT. The Wible et al. (2007a, b) cladograms excluded taxa nesting here with *Maelestes*: IVPP V2385 (Ting et al., 2004) and *Anagale*. The LRT includes *Asioryctes*, which nests a few nodes outside the last common ancestor of all placental mammals, as in Wible et al. (2007a, b). On *Anagale* the primordial nuchal crest and elongate hoof-like unguals are traits retained by many members of the Tenreketos.

Like the related elephant shrew, *Rhynchotus*, the torso and tail of *Leptictis* (skull 6 cm long) were short and the legs were long with digitigrade extremities and a semi-circular astragalus analogous with those of basal artiodactyls. The long rostrum is retained in descendant taxa.

The next clade includes much larger predatory taxa, *Sinonyx* (skull 28 cm) and *Andrewsarchus* (skull 83 cm long). Both had larger canines and parietal crests, traits retained by descendant taxa.

Two extant tenrecs split off next, *Tenrec* (Fig. 2) and *Hemicentetes*. Both have tiny tails, a derived trait. Related extinct taxa, *Indohyus* and *Lepticitidium* retained and further developed long tails. Both were the first aquatic taxa in the Tenreketos. Today tenrecs are found in Madagascar. *Indohyus* fossils are found in Kashmir. These landmasses and their occupants split apart 89–85 million years ago (McKenzie Sclater, 1971; de Wit, 2003), pushing this node back twenty million years before the Late Cretaceous extinction event.

Hemicentetes is known to make short duration tongue clicks (5000–17,000 cps) that aid in echolocation (Gould, 1965). Odontocetes echolocate by producing short duration clicks using ‘phonic lips’ located in the melon along the nasal passage outside of the skull (Cranford, 2000). Given the close phylogenetic relationship of tenrecs and odontocetes in the LRT, echolocation in odontocetes likely originated with Late Cretaceous tenrecs similar to *Hemicentetes* and *Indohyus*.

Tenrecs typically travel and feed in family/social groups of kinship litters (Gould and Eisenberg, 1966). Many skeletons of *Indohyus* were washed together, buried in freshwater stream sediments (Thewissen et al., 2009). Given their close phylogenetic relationship in the LRT, these kinship litters may be retained as pods in living odontocetes.

In the semi-aquatic tenrec, *Indohyus,* the tail is long, but not longer than the hind limb. The hind limb is slightly longer than the fore limb. The paddle-like pes is substantially larger than the manus. The limbs are made of denser bone with less marrow, making them better suited to wading and swimming in lake shallows (Thewissen, et al. 2009). Unique among terrestrial taxa, the middle ear has a thickened internal lip, as found in cetaceans. Further evidence for an aquatic habitat comes from the tooth chemistry of *Indohyus* (Thewissen, et al. 2009). Based on its artiodactyl-like ankle, *Indohyus* was earlier assumed to be a small deer-like herbivorous artiodactyl (Thewiessen, et al. 2007). Phylogenetically that is a problem for a piscivorous odontocete ancestor, but not if that ancestor is an insectivorous-grading-to-piscivorous aquatic tenrec. Thewiessen et al. (2009) reported, “This shape of the astragalus, with a proximal trochlea (hinge joint) as well as distal trochlea, only occurs in even-toed ungulates (artiodactyls).” An overlooked convergent shape is also found in *Rhynchocyon* and *Leptictidium*, which also have an ungulate-like digitigrade pes with hooves and elongate metatarsals. The unguals of *Indohyus* were described (Thewiessen et al. 2009) as hooves, elongate and tapering, but with an expanded tip. Such hooves are also present in *Anagale*.

Leptictidium had smaller fore limbs, elongate hind limbs and a muscular tail much longer than its hind limbs. The skull and dentition are close matches to *Tenrec* and *Maiacetus*. Originally considered a bipedal omnivore and saltator, *Leptictidium* had a 'loose' sacroiliac joint, different from those in typical saltators, but similar to those found in so-called 'land whales.' Phylogenetic bracketing, comparative morphology and the fossil's lacustrine matrix indicate *Leptictidium* was aquatic, like its sister *Indohyus*. It could swim by paddling those long hind legs together, coordinated with dorsoventral undulations of that long, muscular tail. This pattern of swimming is further refined in toothed whales.

More derived toothed taxa linking *Pakicetus* to archaoecetes and odontocetes are well documented (e.g. Thewissen, et al. 2009), but in short: the teeth become simple pegs, the external naris and lacrimal migrate over the cranium, the tail enlarges and develops flukes, the forelimbs become flippers, the pelvis is reduced and the hind limbs become internal vestiges.

Mesonyketos

The origin of the traditional clade Mysticeti has been called 'a baffling problem' (Fitzgerald, 2006) largely because relevant taxa have not been included in prior whale analyses (e.g. Marx and Fordyce, 2015). Here that problem is resolved with the addition of previously omitted taxa.

Mesonyx (30 cm skull length) nests at the base of the Mesonyketos. In the LRT mesonychids were derived from basal ungulates of similar size, like *Phenacodus* (late Paleocene). Distinct from *Phenacodus*, *Mesonyx* had a larger skull with a higher parietal crest and larger canines. The mandibular joint was lower. The medial digits were vestigial. Phylogenetic bracketing nests *Mesonyx* in the midst of many large herbivores, so those large canines were likely used for display and fighting, as in the related *Hippopotamus*, than against prey. Exceptionally meat-eating is known in hippos (Dudley, 1996, 1998).

The first taxon to split off is the neotonous *Ocepei*a (9 cm skull). Retaining juvenile traits into adulthood, it had lower skull crests and smaller canines. The orbits were raised to the top of the skull, as in related hippos. The appearance of *Ocepeia* in the Paleocene argues for an earlier appearance of mesonychids than the Eocene.

Hippopotamus (70 cm skull) splits off next. This extant, graviportal herbivore is more at home in the water, but still able to run on land. The orbits are elevated above the elongated and laterally expanded rostrum. The lower incisors are elongate and oriented anteriorly. The ribcage is expanded ventrally and posteriorly, reducing the lumbar region. The tail is a vestige. Hair is nearly absent, but a deep layer of fat is present. Nursing and communication takes place underwater. Some of these traits are retained in descendant mysticetes.

Next in the lineage of mysticetes, *Cambaytherium* (35 cm skull), was originally considered a basal perissodactyl close to anthracobunids (Rose et al., 2014). Fossils were found on the marine coastline of western India, coeval with *Pakicetus*. *Cambaytherium* did not have the dorsal orbits and elongate muzzle of *Hippopotamus*, but it had a large retroarticular process on the dentary, a trait retained in succeeding taxa. The teeth were all more similar in size, lacking giant canines. The putative desmostylian, *Cornwallius* (Hay 1923, Cornwall 1922, Beatty 2006a, b; Early Oligocene) nests with *Cambaytherium* in the LRT. Adults had a downturned rostrum, as in desmostylians. Juveniles did not, as in anthracobunids. The procumbent incisors and canines of *Cornwallius* were separated from the suborbital desmotylian-grade molars by a long diastema (the paraglossal crest). This is the first step toward toothlessness in the lineage of mysticetes.

At the next split, *Anthracobune* (20 cm skull) was originally considered a proboscidean (Pilgrim, 1940), then a perissodactyl (Cooper et al., 2014) before nesting in the LRT between cambaytheres and desmostylians. *Anthracobune* also nests at the base of a small clade that includes toothy *Mammalodon* and *Janjucetus*, taxa known principally from skulls. Both were earlier restored as hydropedal stem mysticetes (Fitzgerald, 2006; Fordyce and Marx, 2016), but phylogenetic bracketing in the LRT indicates these taxa must have had robust limbs. Here the naris opens more dorsally than anteriorly, as in desmostylians and mysticetes.

The basal desmostylian, *Neoparadoxia* (Barnes, 2013) splits off next. Prior studies (Reinhart, 1959; Barnes, 2013) nested desmostylians with sirenians and elephants. Like hippos the orbit of *Neoparadoxia* is elevated. The wide rostrum is downturned and includes a long diastema. The tail is a vestige, but the manus and pes are broad enough to swim with, powered by dorsoventral undulations of the spine and hind limbs (Gingerich, 2005). This behavior would be retained by mysticetes, analogous to the aquatic taxa in the clade Tenreketos.

Closely related *Paleoparadoxia* (50 cm skull), splits off next. The skull is at least twice as wide as tall, as in mysticetes. The orbits are not elevated.

Desmostylus (35 cm skull; Marsh, 1888; Domning, Ray and McKenna, 1986; Uno and Kimura, 2004; Inuzuka 2009) nests at the base of the clade that includes the right whales, *Eubalaena* and *Caperea*. *Desmostylus* has fewer and smaller teeth. The rostrum is narrower than the mandibles, a trait exaggerated in right whales. The wider, flatter cranial roof of *Desmostylus* is retained in descendant right whales. The neck is compressed to less than half the skull length. As in *Caperea*, the lumbar region is reduced to two or three vertebrae in *Desmostylus*. The seven preserved coccygeal and caudal vertebrae are small and flat, extending not much further than the posterior ilium. The metacarpals are flattened, as in mysticete flippers. Compared to *Paleoparadoxia* the limbs in *Desmostylus* are relatively smaller relative to the torso and the hind limbs are shorter than the fore limbs. Distinct from most mammals, the humerus and femur have a sprawling configuration.

The extant pygmy right whale, *Caperea marginata* (Gray, 1846), was recently considered 'the last of the cetotheres' (Fordyce and Marx, 2013), but only in the absence of desmostylians. Here it returns to its traditional nesting with the much larger, extant right whale, *Eubaelana*. Like *Desmostylus*, *Caperea* has seven robust post-sacral vertebrae plus eight smaller caudals between the flukes. The great reduction of the pelvis in *Caperea* changed the coccygeal vertebrae into caudal vertebrae, therby producing a longer practical tail. *Caperera* is toothless, with baleen deeper than its open and unfused mandibles. Like the right whales, it is a ram-feeder on calanoid copepods. The sternal elements and manus were reduced to vestiges compared to *Desmostylus*. Bisconti (2012) noted, "Given that *C. marginata* possesses a mix of balaenid and balaenopterid characters, it is difficult to understand which features are the result of convergence and which are those representing the proof of true phylogenetic relationships." The LRT resolves this issue by nesting plesiomorphic *Caperea* near the base of both major mysticete clades.

In the giant right whale, *Eubalaena,* the jaws are permanently open for ram feeding and giant lower lips rise to close off the sides of the mouth. The lacrimals and frontals extend laterally, matching the wide mandibles. In *Eubalaena* the 16 caudals in series are not longer than the lumbar series, now increased to nine vertebrae. Distinct from all other members of the Mesonyketos, *Caperea* and *Eubalaena* redevelop a tiny manual digit 1.

In the LRT, the taxon *Behemotops* (40 cm skull) is scored based on the narrow skull of the RBCM.EH2007.008.0001 specimen (Fig. 3; Beatty and Cockburn, 2015), which does not match several wide and toothy dentaries previously assigned to this genus (Domning, Ray and McKenna, 1986). A better fit to the concave maxilla of the RBCM specimen is found in the elongate dentary of the Sanjussen specimen cf. of *Vanderhoofius* sp. (UHR32380, Fig. 3, Uno and Kimura, 2004; Chiba et al., 2015), which does not have a strong medial symphysis, as in mysticetes. *Behemotops* was originally considered the most primitive desmostylian based on wide toothy mandibles, but the RBCM specimen nests between *Desmostylus* and all other (non-right whale) mysticetes in the LRT. The post-crania of the RBCM specimen are poorly known: some dorsal vertebrae, a distal scapula and a large humerus that could be semi-terrestrial or hydropedal.

Distinct from all prior whale studies, toothless *Miocaperea* (Bisconti 2012; late Miocene, 7–8 Ma; 1m skull length) nests at the base of all tested non-right whale mysticetes, not with *Caperea* (contra Bisconti 2012, who omitted desmostylians). *Miocaperea* is known from a skull three times the length of the *Behemotops* skull, but broadly similar is morphology. Short patches of baleen are preserved. Like hydropedal mysticetes, the orbit migrates posteriorly. A vestige of the jugal appears on the anterior tip of the squamosal. Compared to the RBCM specimen of *Behemotops*, maxillary tusks are absent in *Miocaperea*. The frontals, lacrimals and squamosals are laterally expanded. The parietals do not appear to be roofed over by the supraoccipital to the extent illustrated by Bisoconti (2012). Rather the supraoccipitals appear to extend no further than the anteriormost extent of the squamosal as in *Isanacetus.*

In the LRT taxa preceding the RBCM specimen of *Behemotops* and *Miocaperea* have robust limbs with free fingers. Taxa succeeding these taxa have hydropedal forelimbs without free fingers and vestigial hind limbs that do not emerge from the body wall. The transition from one body type to the other occurred between these two taxa. With *Behemotops* in the Early Oligocene and *Miocaperea* in the Late Miocene, about 20 million years is available for this transition, unless these two are late survivors of an earlier radiation.

Higher tested mysticetes split between cetotheres (*Cetotherium* + (*Tokarahia* + *Yamatocetus*) and *Eschrichtius* + rorquals + (*Isanacetus* + *Balaeonoptera*). *Cetotherium* has 15-16 caudals and the series is no longer than the lumbar section of the torso.

Other than *Miocaperea, Eschrichtius* appears to be the most primitive member of this clade. Relicts of procumbent desmostylian tusk alveoli are present at the anterior tips of the dentaries and maxillae (Fig. 3). Blood vessels and nerves still pass through these openings as they did when tusks were present. *Eschrichtius* is the only baleen whale that still scoops up sediments from the sea floor, similar to behavior imagined for shovel-tusked desmostylians and, by phylogenetic bracketing, *Miocaperea*. *Eschrichtius* has 28 caudals nearly equal to its entire thorax length.

Isanacetus laticephalus (Kimura and Ozawa, 2002) has a skull similar in size to that of *Miocaperea*. The rostrum and frontals are wider. The orbit is stationed more anteriorly. The naris and nasals are narrower. The posterior squamosal descends and the parietal raises diagonal nuchal crests. In palatal view the maxillae are in contact medially.

Extinct cetotheres, like *Yamatocetus* (Early Oligocene), *Tokaraharia* (late Oligocene) and *Cetotherium* (late Miocene) had relatively straight jaw rims with a high cornoid process, distinct from the more plesiomorphic ventrally concave maxillae of rorquals, right whales and *Behemotops.* Thus cetotheres were not ancestral to extant mysticetes and do not nest as transitional taxa arising from the toothed archaeocete, *Aetiocetus* (contra Emlong, 1966; Van Valen 1968; Geisler et al. 2011).

Embryological studies

In a study of embryo bowhead whales (genus: *Balaena*), Thewissen et al. 2017 noted the rack of baleen was “implanted more or less where the tooth rows would be, but there is no trace of teeth.” By following the hypothesis of an archaeocete origin for mysticetes, they came to realize, “The pattern of dental evolution in mysticetes is thus counterintuitive, first the number of teeth increases in evolution but then teeth disappear altogether suddenly.” By contrast, in the present hypothesis where mysticetes evolve from desmostylian ancestors, adult teeth and tusks disappear in the jaws gradually and leave traces of their departure.

Thewissen et al., 2017 reported 41 upper and 35 lower tooth ‘caps’ in each jaw of an embryo bowhead whale. Where do such large numbers come from? In the LRT there are no tetrapods in the lineage of whales with more than 30 teeth in the maxilla, until one extends the search to the pre-tetrapods, *Tiktaalik* and *Panderichthys*.

Peredo et al. (2017) provided a comprehensive review of the literature on tooth buds and concluded, “Based on the available range of evidence, the origin and evolution of baleen in mysticetes defies simple explanations.” The Peredo team did not consider desmostylians, but held to the archaeocete hypothesis of mysticete origins.

In the LRT, the origin of baleen in mysticete whales can be traced to the narrowing of the rostrum, the widening of the mandibles, the disappearance of the premolars (= appeance of the long diastema), the reduction of all teeth and tusks along with the increasing lateral exposure of the palatal portion of the ventrally concave maxilla in desmostylians. That’s the simple explanation that comes with taxon inclusion.

DNA and supermatrix studies

Gatesy (1997) used molecules to nest hippos with whales (Balaenopteridae + (Delphinoidea + Physeteridae)). A long list of artiodactyls nested elsewhere. Their short tree topology matches the LRT sans tenrecs. Tenrecs were not tested by Gatesy (1997).

Geisler et al., (2011) created a supermatrix of traits, but omitted tenrecs and desmostylians from their taxon list. By default (due to taxon exclusion) the anthracobunids, *Janjucetus* and *Mammalodon,* nested between the toothed whales, *Zygorhiza* and (*Chonecetus* + *Aetiocetus*). These are wrongly considered the last taxa with teeth in the Geisler et al. lineage of mysticetes. There is no demonstrated gradual loss of teeth in the Geisler et al. lineage. Their basalmost mysticetes include the flat-jawed and toothless cetotheres *Eomysticetus, Micromysticetus, Diorocetus* and *Pelocetus* nesting prior to the extremely derived, bow-skulled right whale, *Eubaleaena*. Once again, there is no gradual accumulation of traits between transitional taxa in the Geisler et al. cladogram. The primitive gray whale, *Eschrichtius*, nests at the third derived node in their Mysticeti. So, their cladogram essentially reverses the order of mysticetes recovered by the LRT, putting derived taxa in basal nodes and vice versa.

CONCLUSIONS

The addition of relevant taxa nests odontocetes and mysticetes in two clades derived from predatory and non-predatory limbed ancestors. This invalidates the results of earlier, smaller studies that nested mysticetes with odontocetes, archaeocetes and artiodactyls when relevant taxa were excluded. Here the Odontoceti arise from aquatic echolocating tenrecs and their kin. Here the Mysticeti arise from increasingly toothless desmostylians and their kin. This report documents the gradual accumulation of derived traits that led to the Odontoceti and the largely convergent Mysticeti.

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Figure captions

Figure 1.

Subset of the large reptile tree, (= LRT; www.ReptileEvolution.com/reptile-tree.htm), focusing on the two whale clades, Odontoceti and Mysticeti and their proximal outgroups. See link above for complete taxon list.

Figure 2.

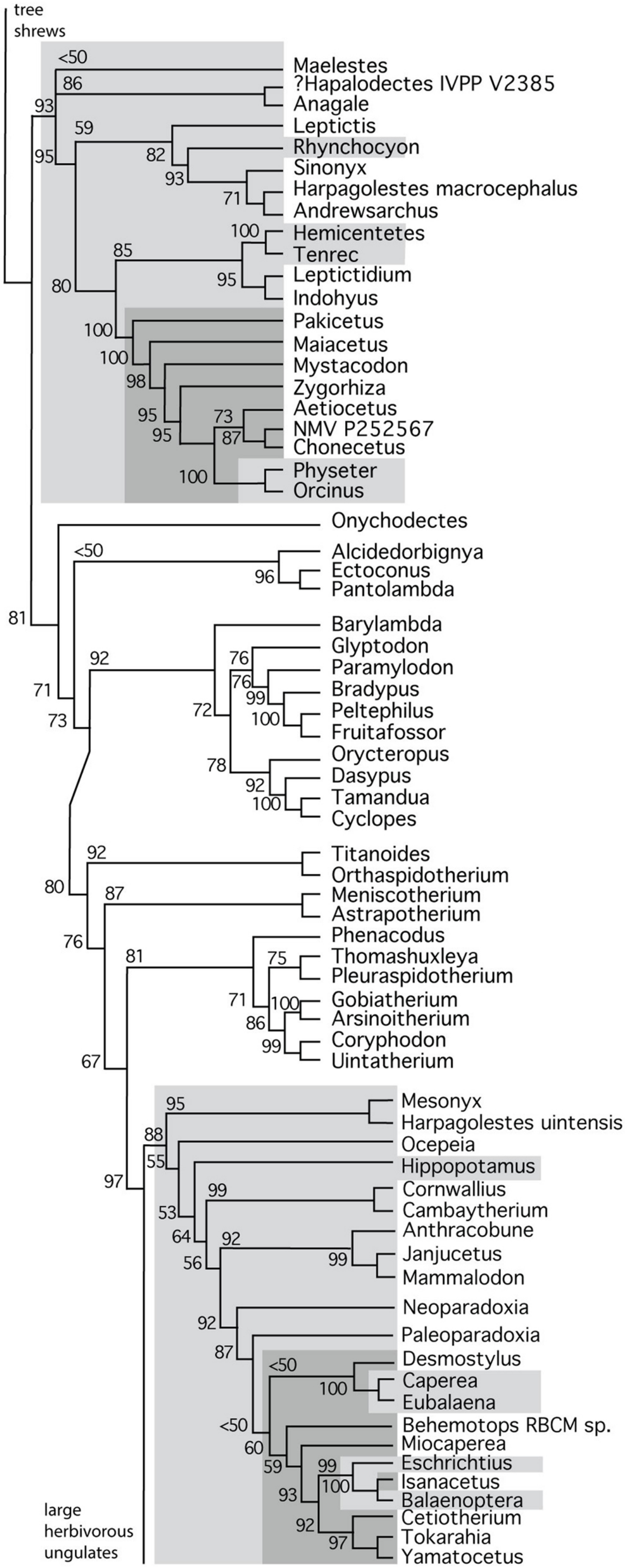
Comparative lateral views of two taxa in the tenrec/odontocete clade. Above: The extant tenrec, *Tenrec*. Below: The much larger ‘whale with legs’, *Maiacetus* (Eocene). Inside the jaws of *Maicetus* is the skull of *Tenrec* to scale.

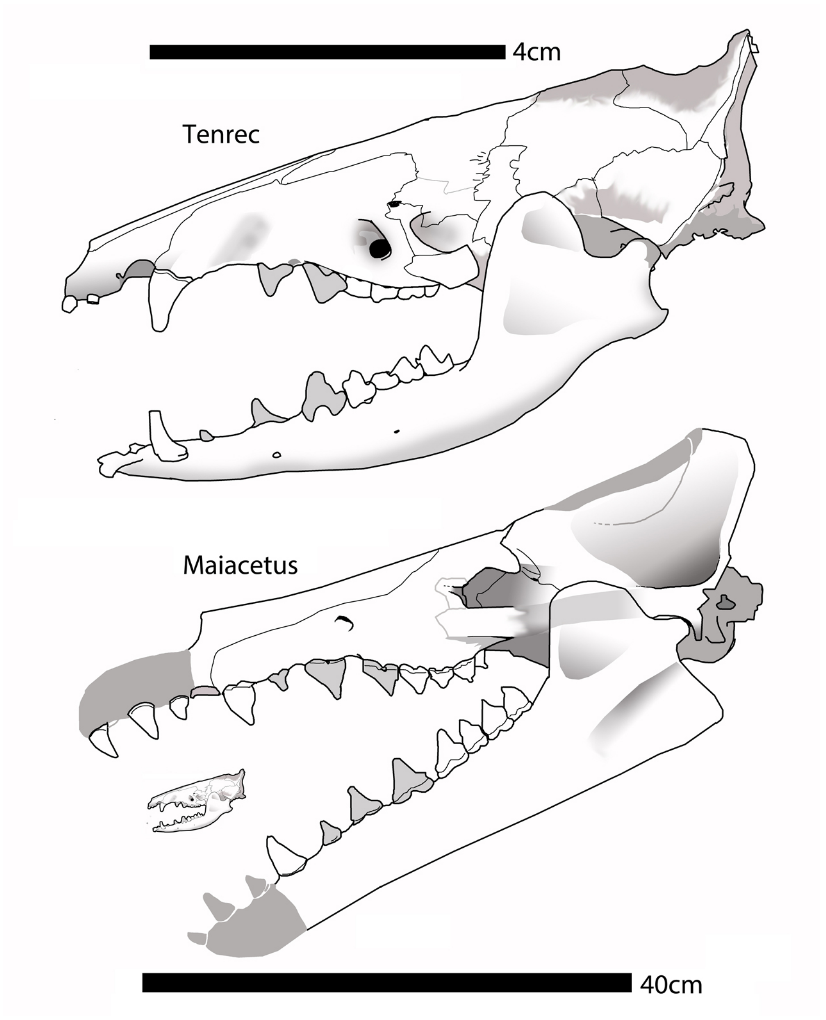
Figure 3.

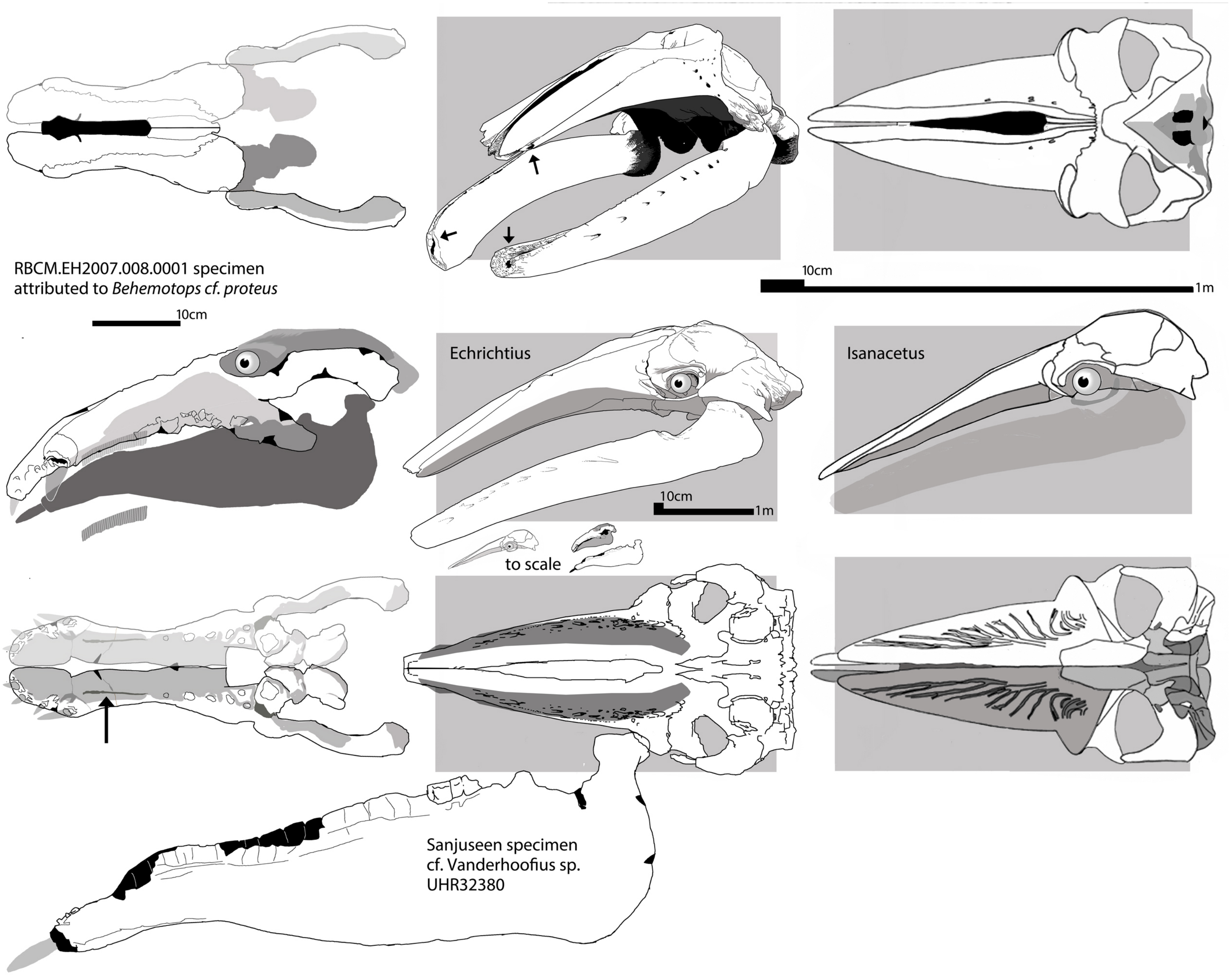
Three taxa in the mesonychid/mysticete clade at the transition from desmostylians to mysticetes: Left column: The RBCM skull originally attributed to *Behemotops* in dorsal, lateral and palatal views along with the Sanjussen mandible scaled down to fit the skull (dark gray). Bottom left column: The Sanjussen mandible specimen to scale with the RBCM skull. Middle column: The gray whale (genus: *Echrichtius*) in anterior view. Arrows point to former tusk alveoli. Lateral view of *Isanacetus* and the RBCM specimen to scale. Palatal view of same with baleen in dark gray. Right column: The small baleen whale, *Isanacetus*, skull in dorsal, lateral and palatal views. More extensive nutrient foramina here root baleen to the palate.

Figure 4.

The reduction/retreat of the canine tusk in *Desmostylus* is shown here (upper arrow). Lower arrow points to dentary tusks. Compare to *Eschrichtius* in figure 3.


tree shrews
Maelestes
?Hapalodectes IVPP V2385
Anagale
Leptictis
Rhynchocyon
Sinonyx
Harpagolestes macrocephalus
Andrewsarchus
Hemicentetes
Tenrec
Leptictidium
Indohyus
Pakicetus
Maiacetus
Mystacodon
Zygorhiza
Aetiocetus
NMV P252567
Chonecetus
Physeter
Orcinus
Onychodectes
Alcidedorbignya
Ectoconus
Pantolambda
Barylambda
Glyptodon
Paramylodon
Bradypus
Peltephilus
Fruitafossor
Orycteropus
Dasypus
Tamandua
Cyclopes
Titanoides
Orthaspidotherium
Meniscotherium
Astrapotherium
Phenacodus
Thomashuxleya
Pleuraspidotherium
Gobiatherium
Arsinoitherium
Coryphodon
Uintatherium
Mesonyx
Harpagolestes uintensis
Ocepeia
Hippopotamus
Cornwallius
Cambaytherium
Anthracobune
Janjucetus
Mammalodon
Neoparadoxia
Paleoparadoxia
Desmostylus
Caperea
Eubalaena
Behemotops RBCM sp.
Miocaperea
Eschrichtius
Isanacetus
Balaenoptera
Cetiotherium
Tokarahia
Yamatocetus
large herbivorous ungulates


4cm
Tenrec
Maiacetus
40cm


RBCM.EH2007.008.0001 specimen
attributed to *Behemotops cf. proteus*
10cm
10cm
1m
Echrichtius
10cm
1m
Isanacetus
to scale
Sanjuseen specimen
cf. Vanderhoofius sp.
UHR32380