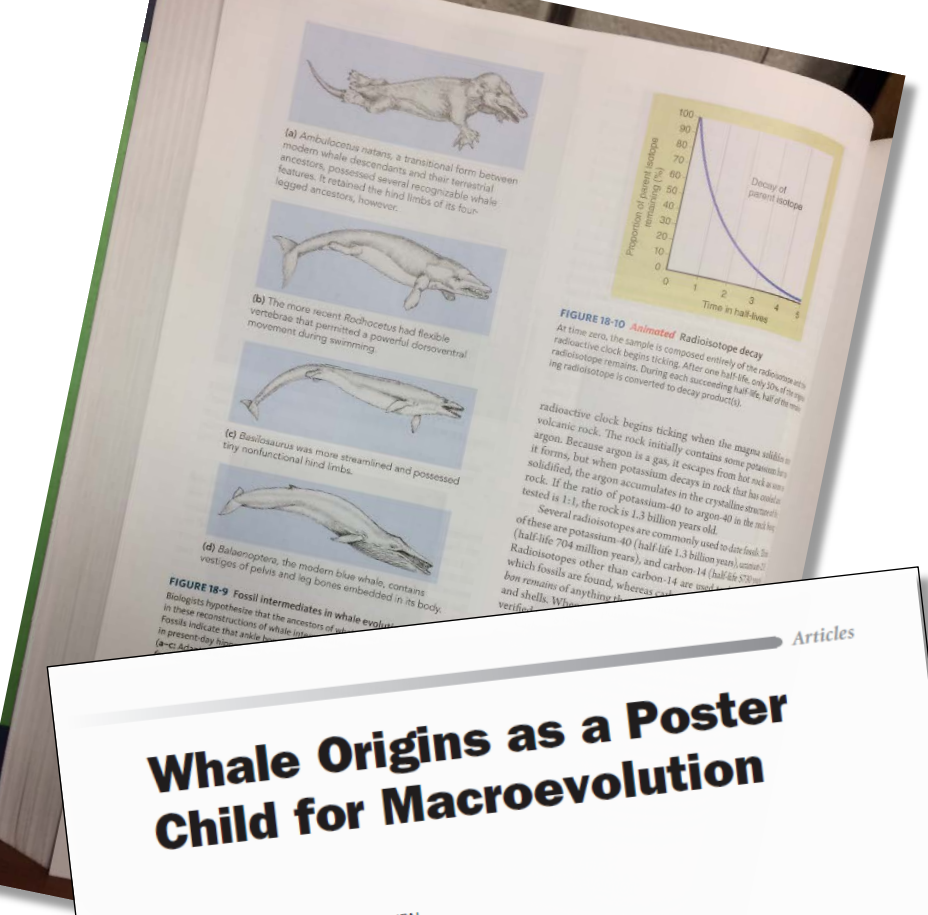
The remarkable tale of the whale: fossils, DNA, isotopes, and the many facets of cetacean evolution

Ryan M. Bebej, Ph.D.
Department of Biology
Calvin College
April 28, 2017

Calvin COLLEGE 1876

BIOLOGOS Voices

Reconstruction of *Kutchicetus* by Lucas Lima



Articles

Whale Origins as a Poster Child for Macroevolution

J. G. M. THEWISSEN AND SUNIL BAJPAI

Whales indisputably are mammals, which is clear from their means of oxygen intake (they breathe with lungs), their care of newborns (mothers nurse their calves with milk), and a host of other features. This implies that whales evolved from other mammals and, because ancestral mammals were land animals, that whales had land ancestors. What happened in the transition to life in the ocean has been hard to imagine for scientists and laypeople alike. In the first edition of the *Origin of Species* (1859), Darwin suggested that a bearlike animal swimming with an open mouth might be a precursor of a filter-feeding baleen whale. This statement attracted much ridicule; in a letter, Darwin observed, "It is laughable how often I have been attacked and misrepresented about this bear" (Gould 1995). In later editions, Darwin deleted this reference to evolution entirely and merely noted that a bear sifting water for insects is "almost like a whale."

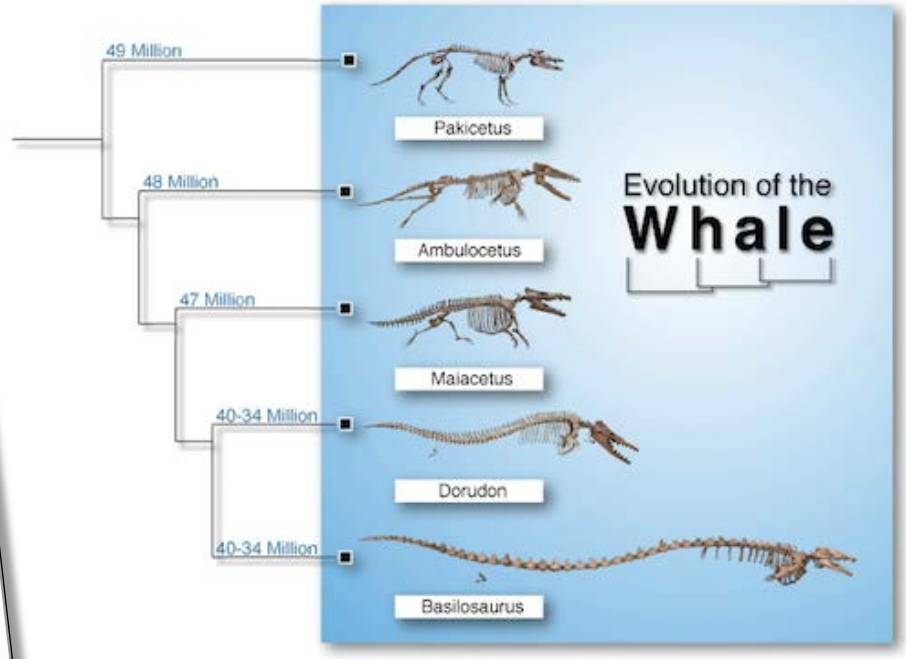
Nearly 150 years later, we can fill in much of the gap that embarrassed Darwin. The last two decades have witnessed an explosive growth in the number of fossils documenting the origins of Cetacea (whales, dolphins, and porpoises). An excellent morphological series of transitional cetaceans is now available to document the transition from land to sea, and many sophisticated analyses detail the biology of these archaic

FOSSILS COLLECTED IN THE LAST DECADE DOCUMENT THE WAYS IN WHICH CETACEA (WHALES, DOLPHINS, AND PORPOISES) BECAME AQUATIC, A TRANSITION THAT IS ONE OF THE BEST DOCUMENTED EXAMPLES OF MACROEVOLUTION IN MAMMALS

ignorance on the part of those unaware of published research. However, the sheer volume and pace of recent research also cause problems. For those outside of the circle of specialists actively studying whale origins, it is hard to keep up with all the new discoveries.

In this article, we first introduce the families of archaic cetaceans that lived in the Eocene (approximately 55 million to 34 million years ago), the oldest period from which cetaceans are known. After that, we discuss the several organ systems that underwent dramatic changes. Then, we put the functional morphology and evolution of two organ systems, locomotion and osmoregulation, in a broader perspective. We

BIOLOGOS



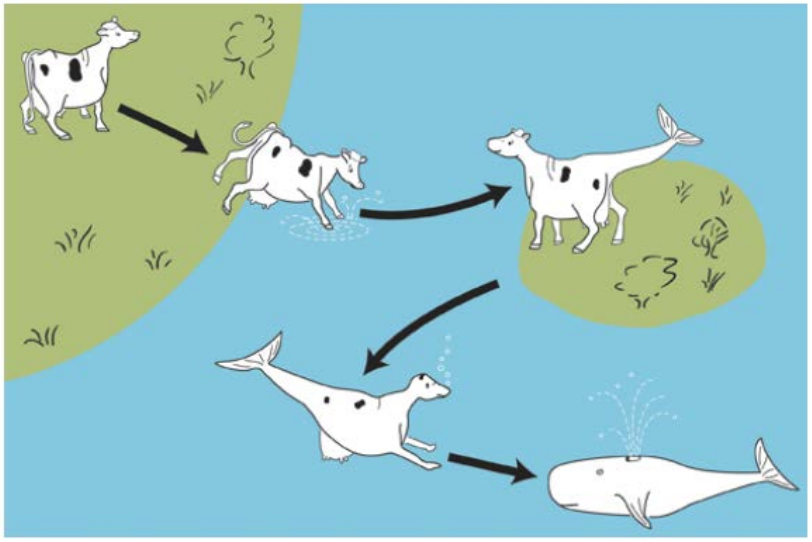
CREATION MINISTRIES INTERNATIONAL

Whale evolution fraud

Another evolutionary icon bites the dust

by Don Batten

First published: 12 April 2014 (GMT+10)
Updated from *Creation* **36**(4):34–35; January 2016



Major Evolutionary Blunders: Are Whales and Evolution Joined at the Hip?

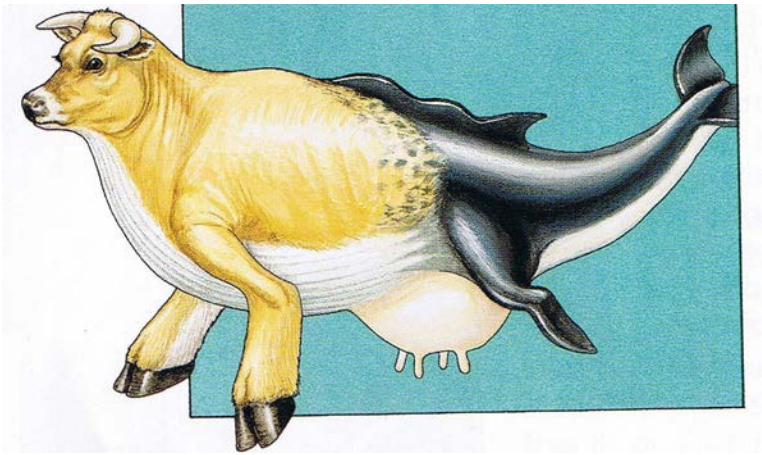
by Randy J. Guliuzza, P.E., M.D. *

Evidence for Creation

ICR INSTITUTE FOR CREATION RESEARCH

"Transitional forms here differ from the University of Michigan depiction … in being *dairy* whales"

– Sunderland (1984)



Outline

I. Brief introduction to cetaceans

II. Historical perspectives on cetacean origins

III. Various facets of cetacean evolution

   a. Fossil record of archaeocetes

   b. Ancient environments and biogeography

   c. Comparative anatomy and development

   d. Genetics and genomics

IV. Summary and concluding remarks

What is a whale?

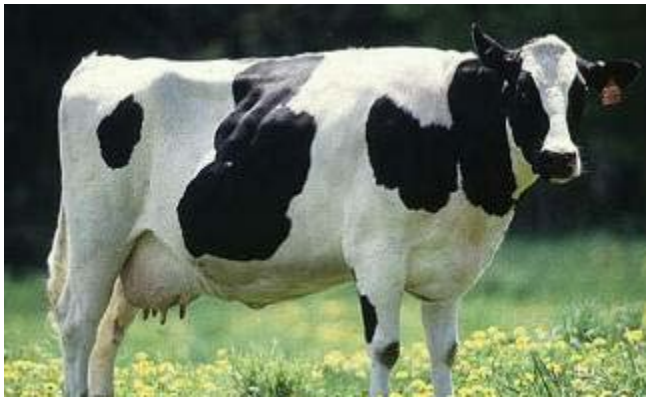
- Whales are **MAMMALS**
  - Breathe atmospheric oxygen
  - Feed their young with milk from mammary glands
  - Live birth with placenta
  - Baleen (hair) in some
  - Large brains
  - Many skeletal features
    - Double occipital condyle
    - Dentary-squamosal jaw joint
    - Three middle ear bones
    - Socketed teeth in some
    - …and many more

But whales are also

SECONDARILY AQUATIC

Most mammals are **TERRESTRIAL**









Some mammals are **SECONDARILY AQUATIC**



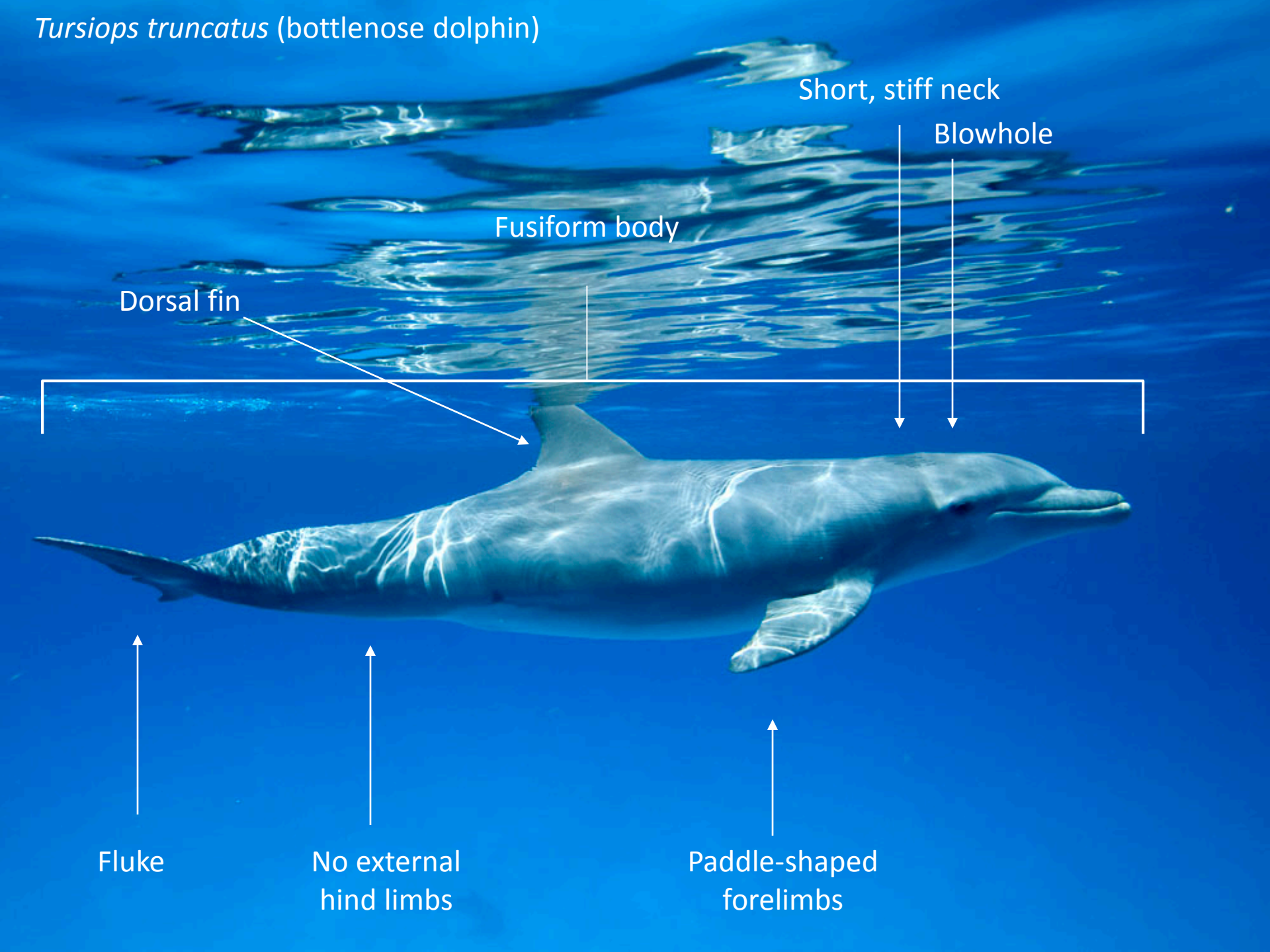




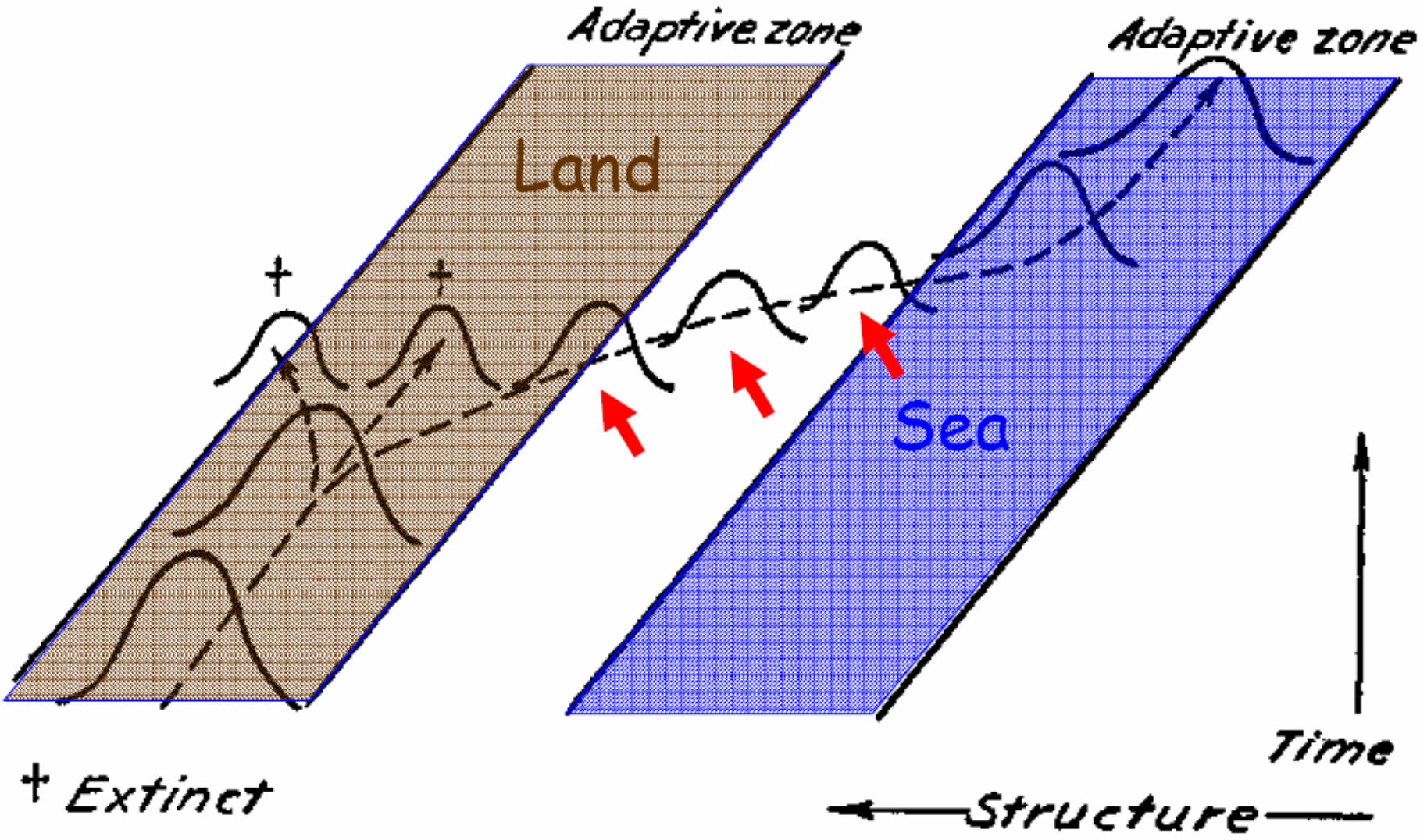

Order Cetacea (Latin: *cetus* = whale)

Odontocetes (toothed whales)

Mysticetes (baleen whales)


Tursiops truncatus (bottlenose dolphin)
Short, stiff neck
Blowhole
Fusiform body
Dorsal fin
Fluke
No external hind limbs
Paddle-shaped forelimbs

Drastic change in adaptive zone

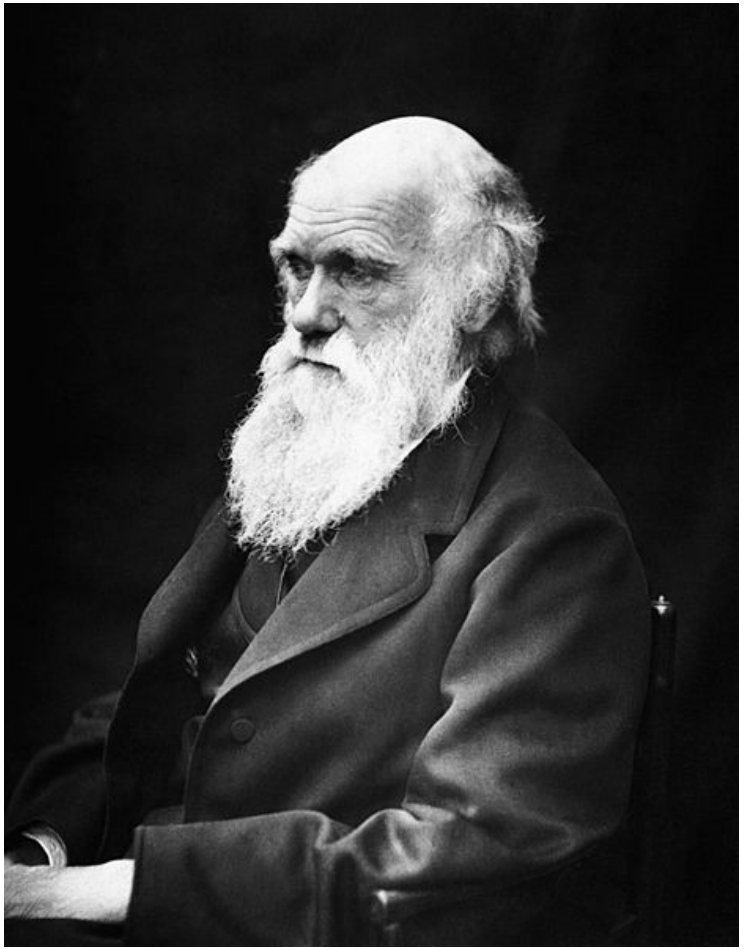


Simpson 1944; Gingerich 2007

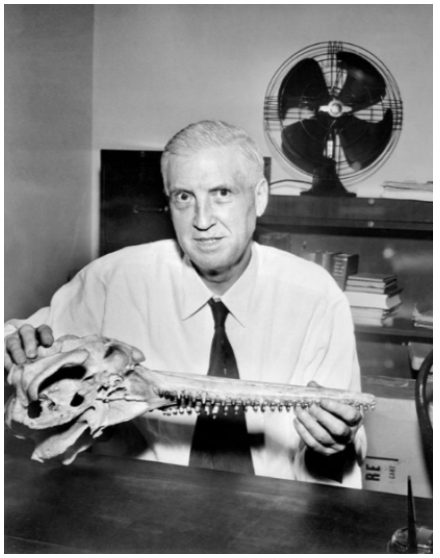
1859: Charles Darwin

"In North America the black bear was seen by Hearne swimming for hours with widely open mouth, thus catching, like a whale, insects in the water. Even in so extreme a case as this, if supply of insects were constant, and if better adapted competitors did not already exist in the country, 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."

– from *The Origin of Species* (ch.6)



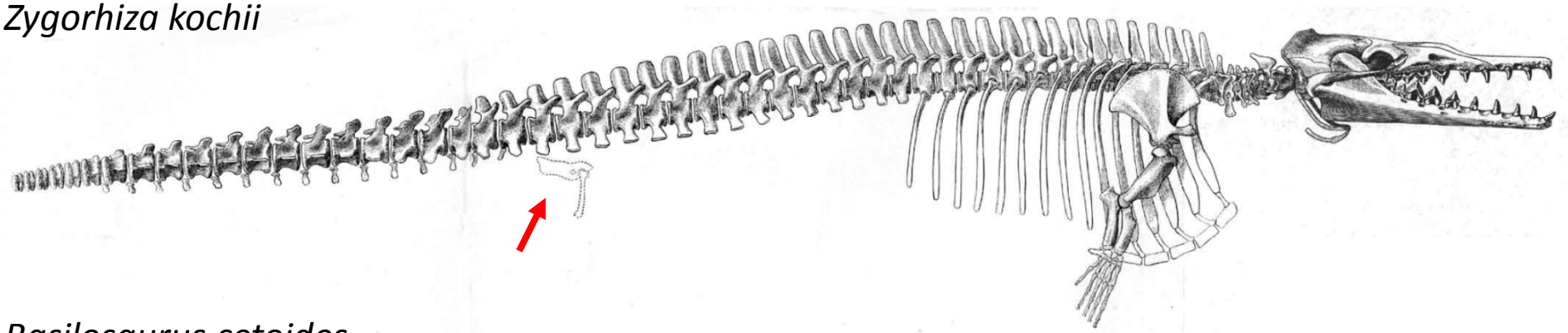
1936: Remington Kellogg



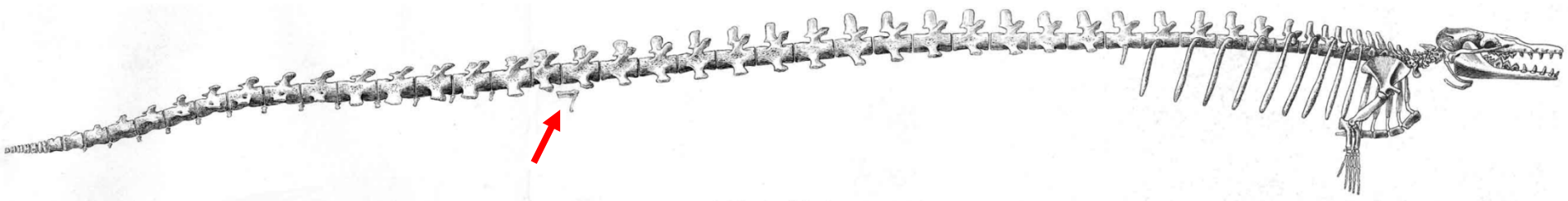
"A Review of the Archaeoceti"

- North American and Egyptian whales
- All clearly fully aquatic

Zygorhiza kochii



Basilosaurus cetoides



Kellogg 1936

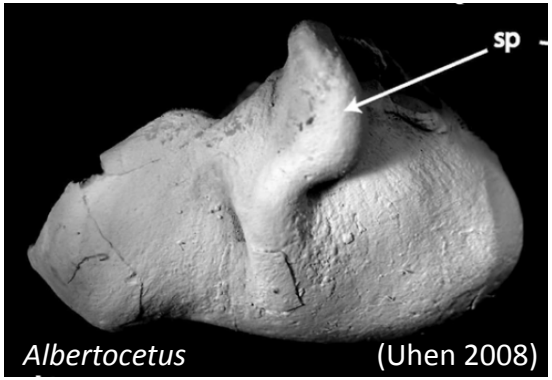
1945: George Gaylord Simpson

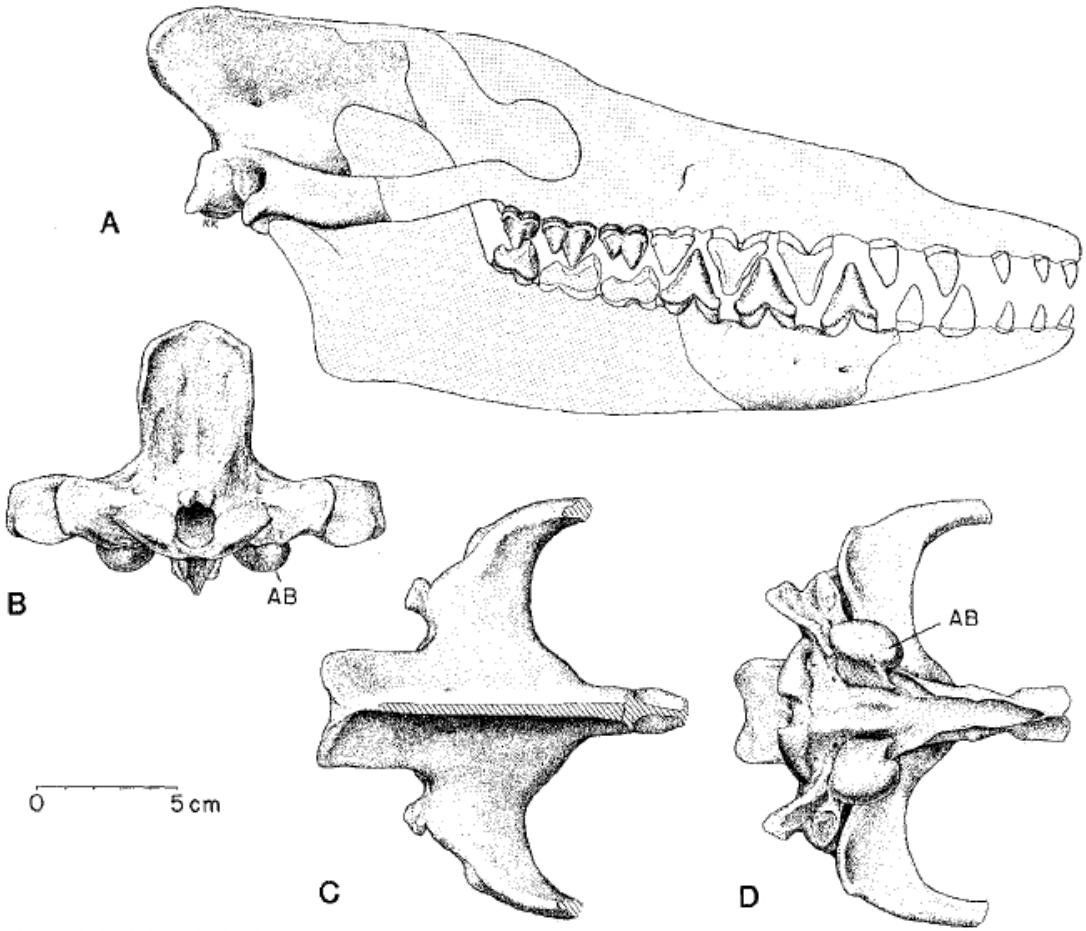
"Because of their perfected adaptation to a completely aquatic life, […] the cetaceans are on the whole the most peculiar and aberrant of mammals. Their place in the sequence of cohorts and orders [of mammalian classification] is open to question and is indeed quite impossible to determine in any purely objective way."

– from *Classification of Mammals*

1981: *Pakicetus inachus*

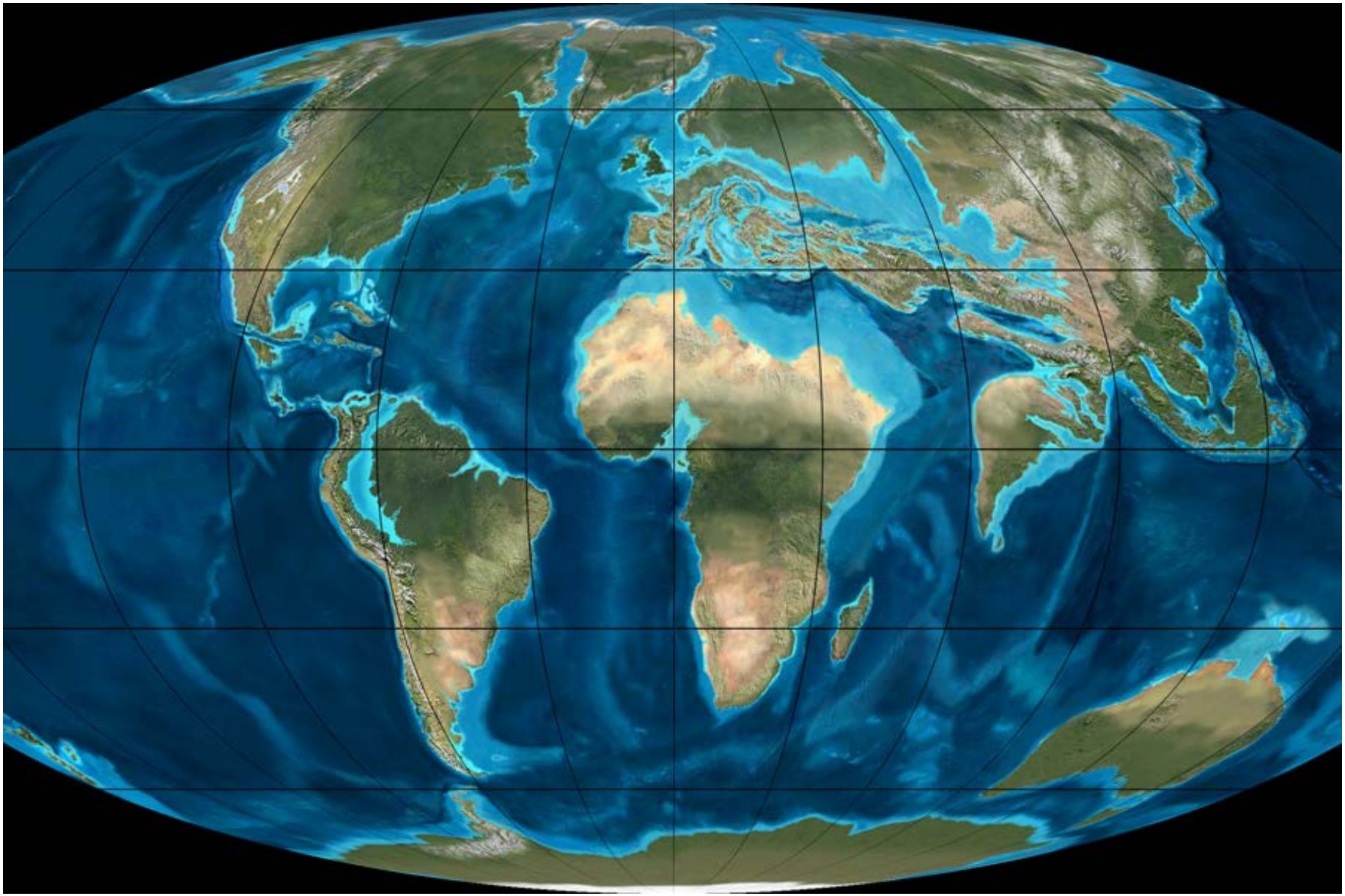
- Pakistan (50 Ma)
- Fluvial sediments bordering ancient Tethys Sea
- Dense auditory bullae other ear features seen ***only in cetaceans***





Gingerich and Russell 1981; Gingerich et al. 1983

Eocene Epoch (50 Ma)



Wadi Al-Hitan (Nov. 2009)

وادي الحيتان

Wadi Al-Hitan (Nov. 2009) وادي الحيتان

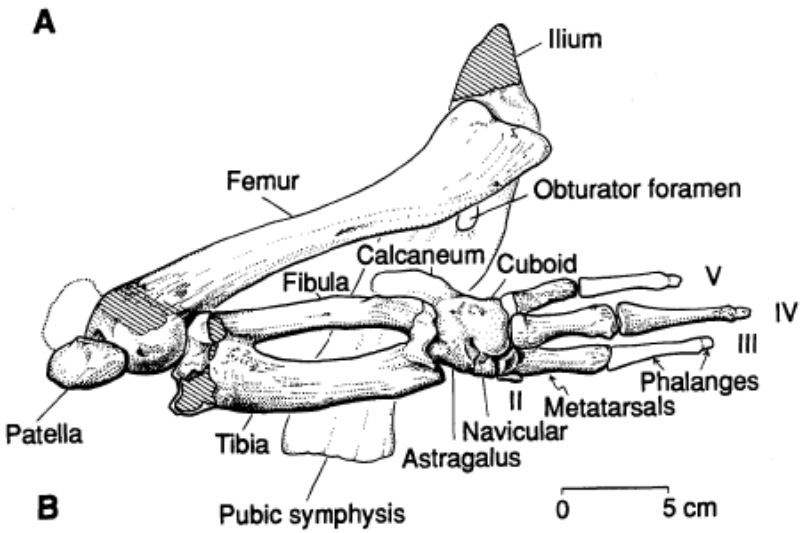
Philip Gingerich holding *Dorudon* vertebrae

Excavating *Basilosaurus isis*, Wadi Al-Hitan (Nov.-Dec. 2009)

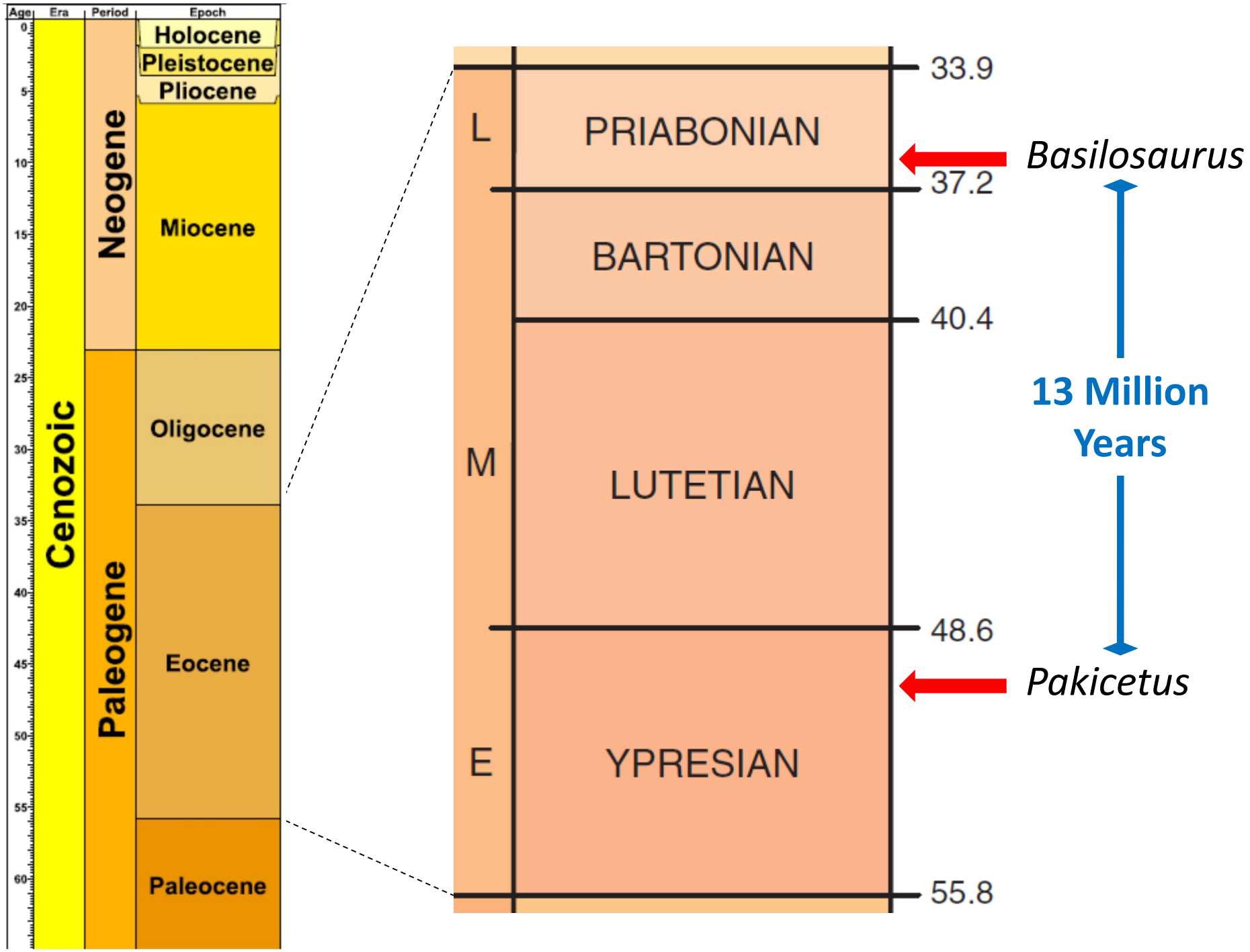
وادي الحيتان

1990: *Basilosaurus isis*

- Egypt (37 Ma)
- Marine shales and sandstones
- Strap-like pelvic bones detached from sacrum, well-formed joint surfaces on femur

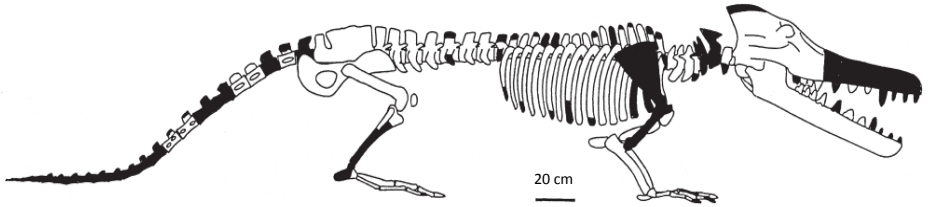


Gingerich et al. 1990

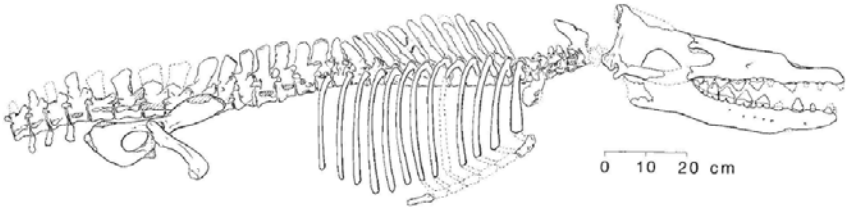

Age
Era
Period
Epoch
Holocene
Pleistocene
Pliocene
Miocene
Neogene
Oligocene
Eocene
Paleocene
Paleogene
Cenozoic
L
M
E
PRIABONIAN
BARTONIAN
LUTETIAN
YPRESIAN
33.9
37.2
40.4
48.6
55.8
Basilosaurus
Pakicetus
13 Million Years

A sampling of archaeocetes…

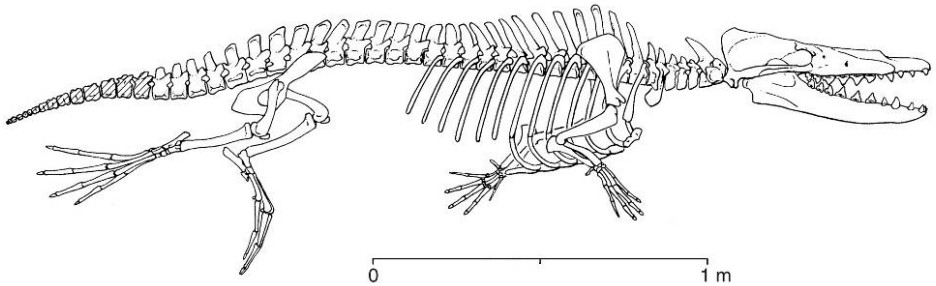
Ambulocetus natans (Thewissen et al. 1994)



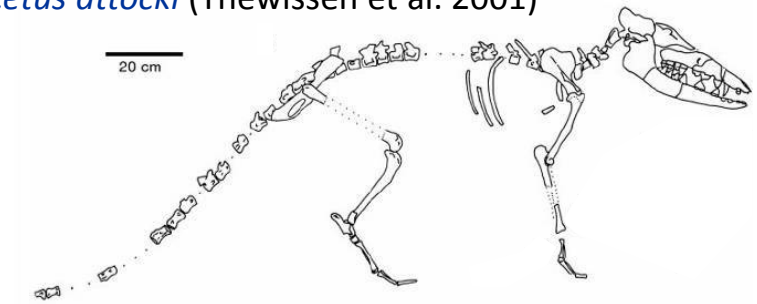
Rodhocetus kasranii (Gingerich et al. 1994)



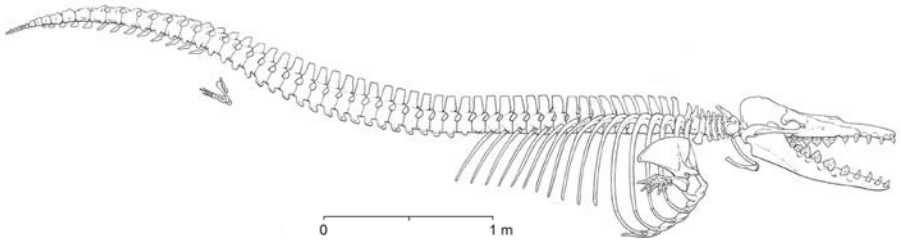
Rodhocetus balochistanensis (Gingerich et al. 2001)



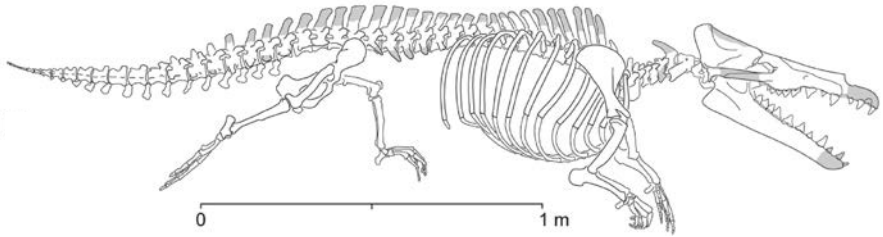
Pakicetus attocki (Thewissen et al. 2001)



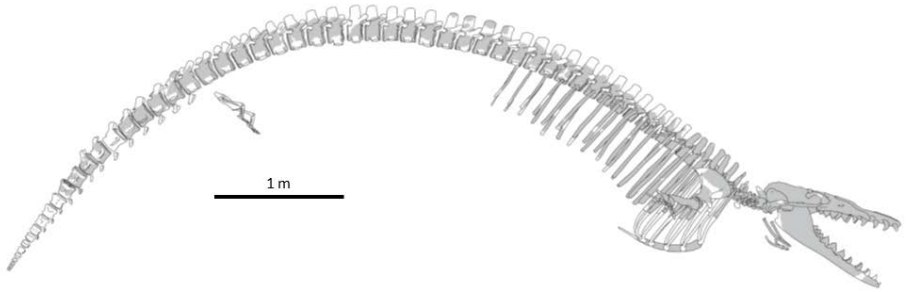
Dorudon atrox (Uhen 2004)



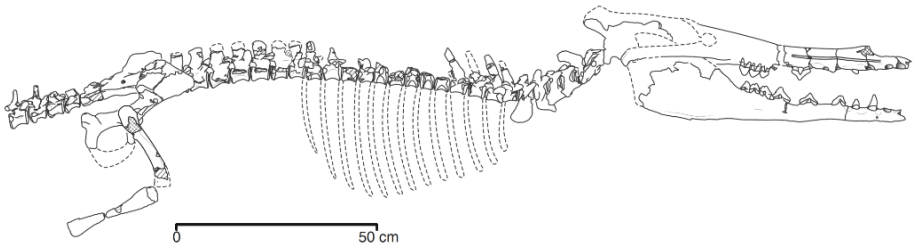
Maiacetus inuus (Gingerich et al. 2009)

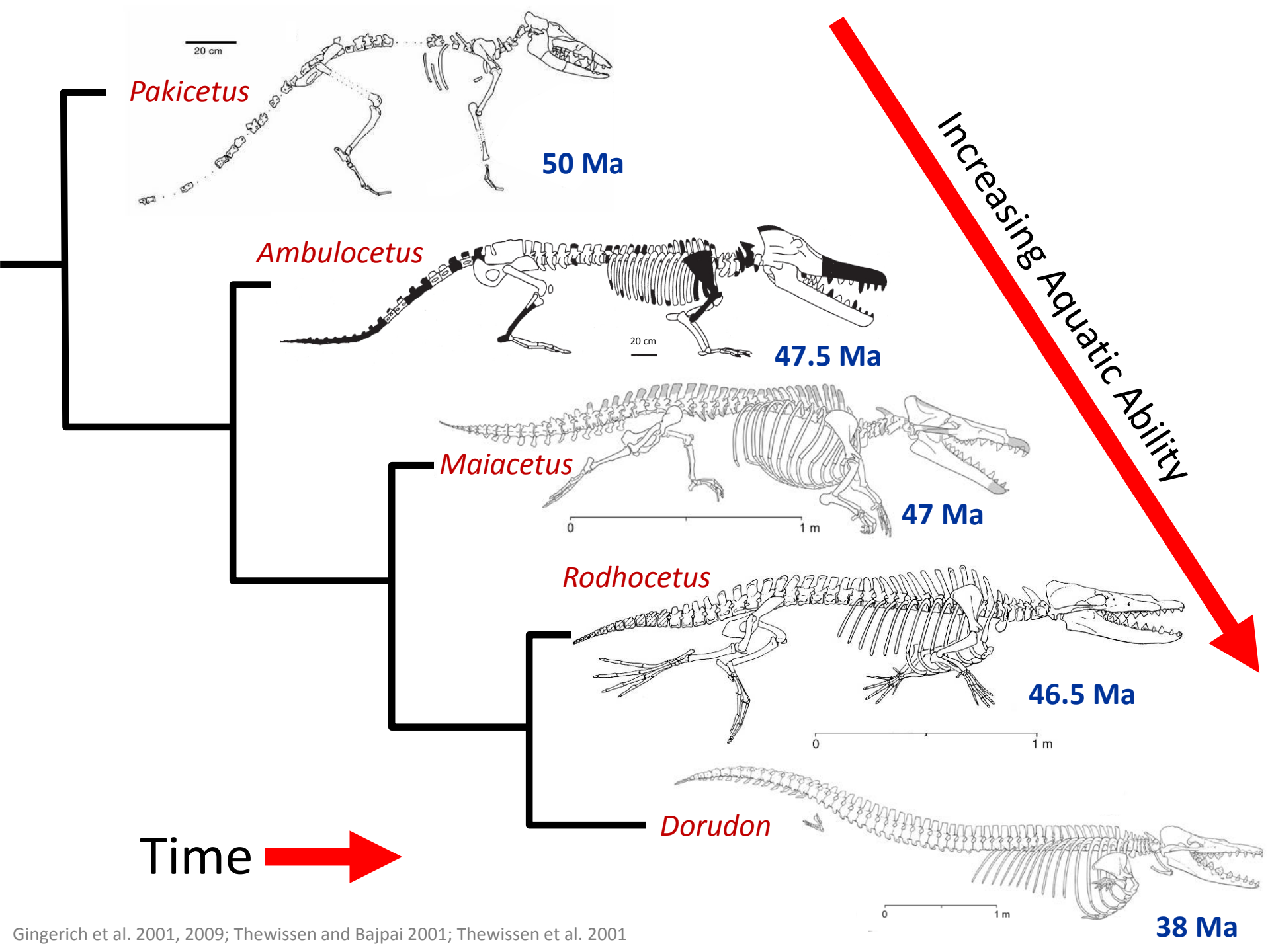


Cynthiacetus peruvianus (Martínez-Cáceres & Muizon 2011)

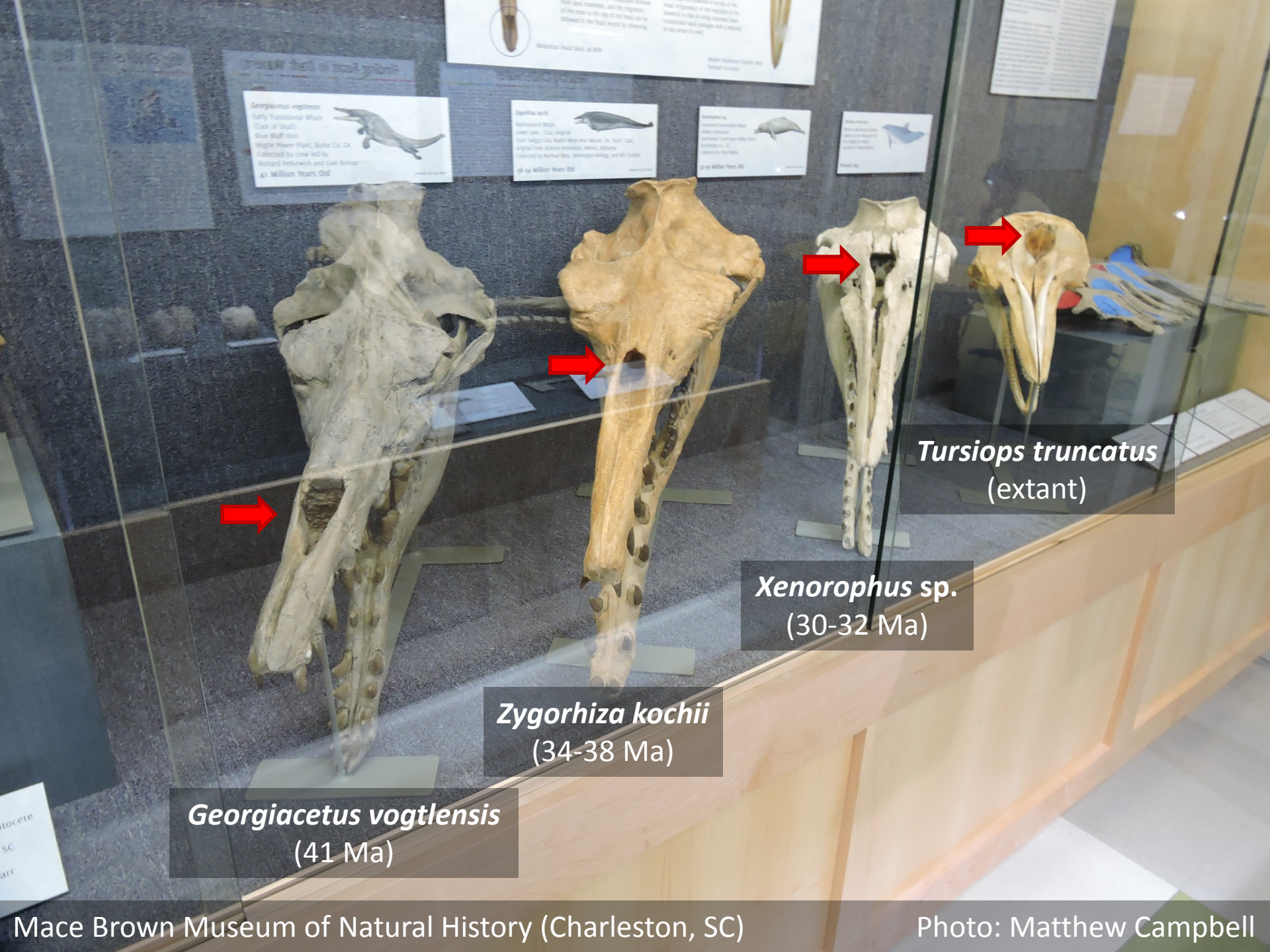


Remingtonocetus domandaensis (Bebej et al. 2012)





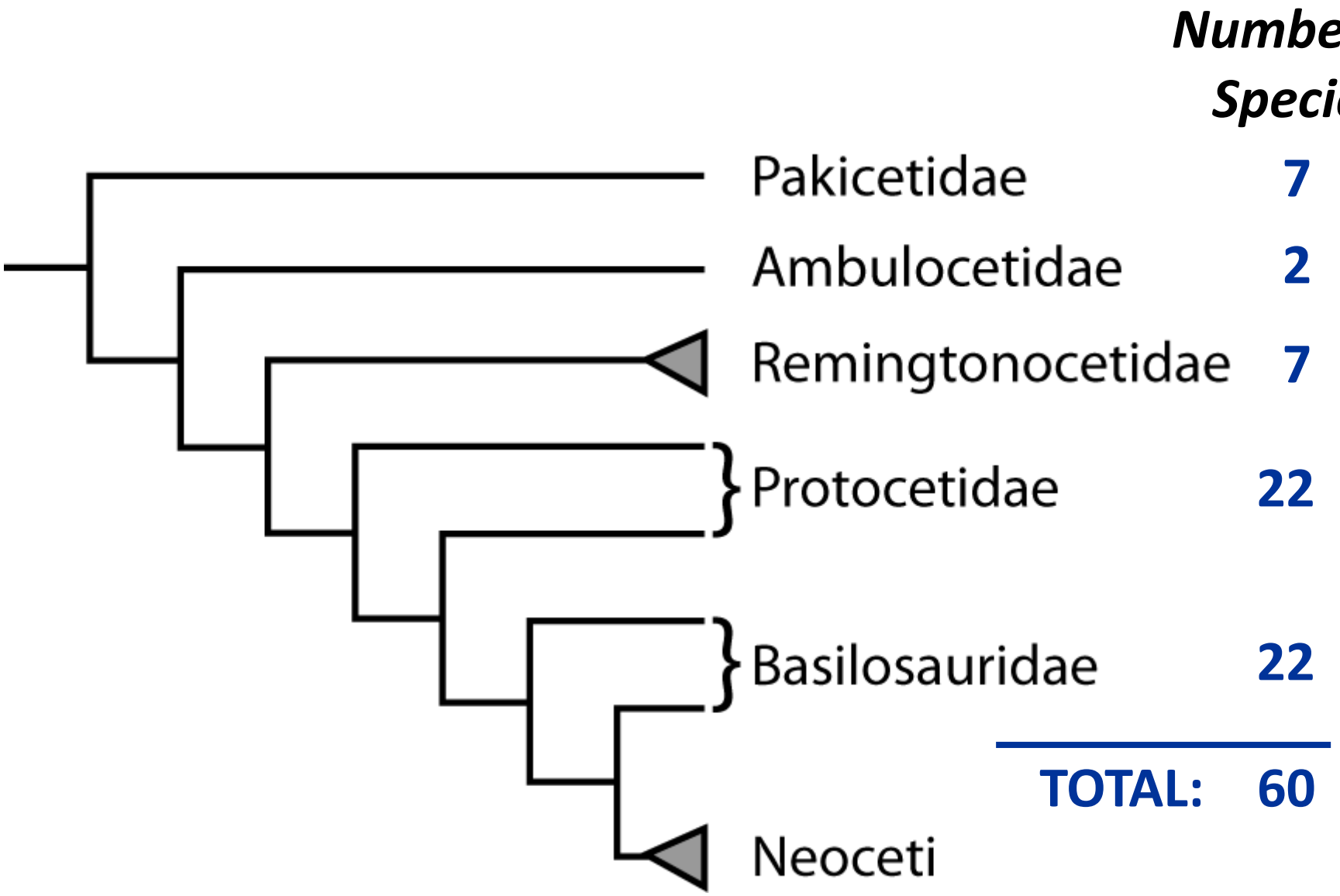
Gingerich et al. 2001, 2009; Thewissen and Bajpai 2001; Thewissen et al. 2001

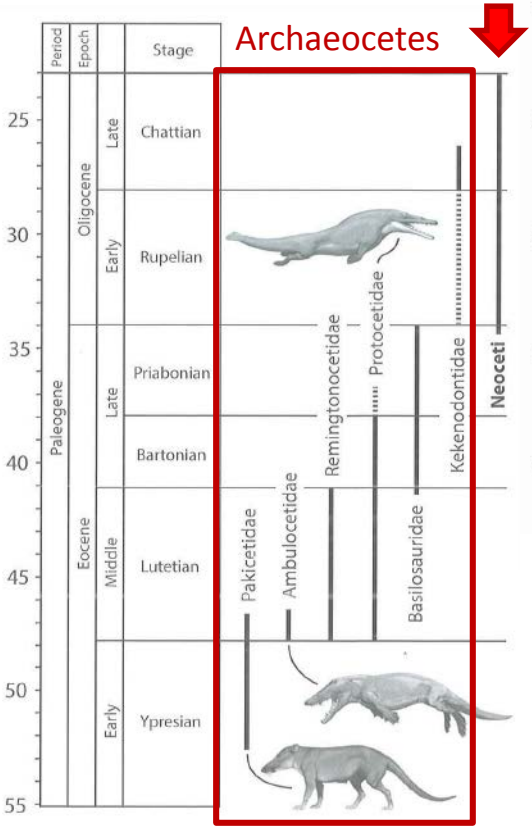


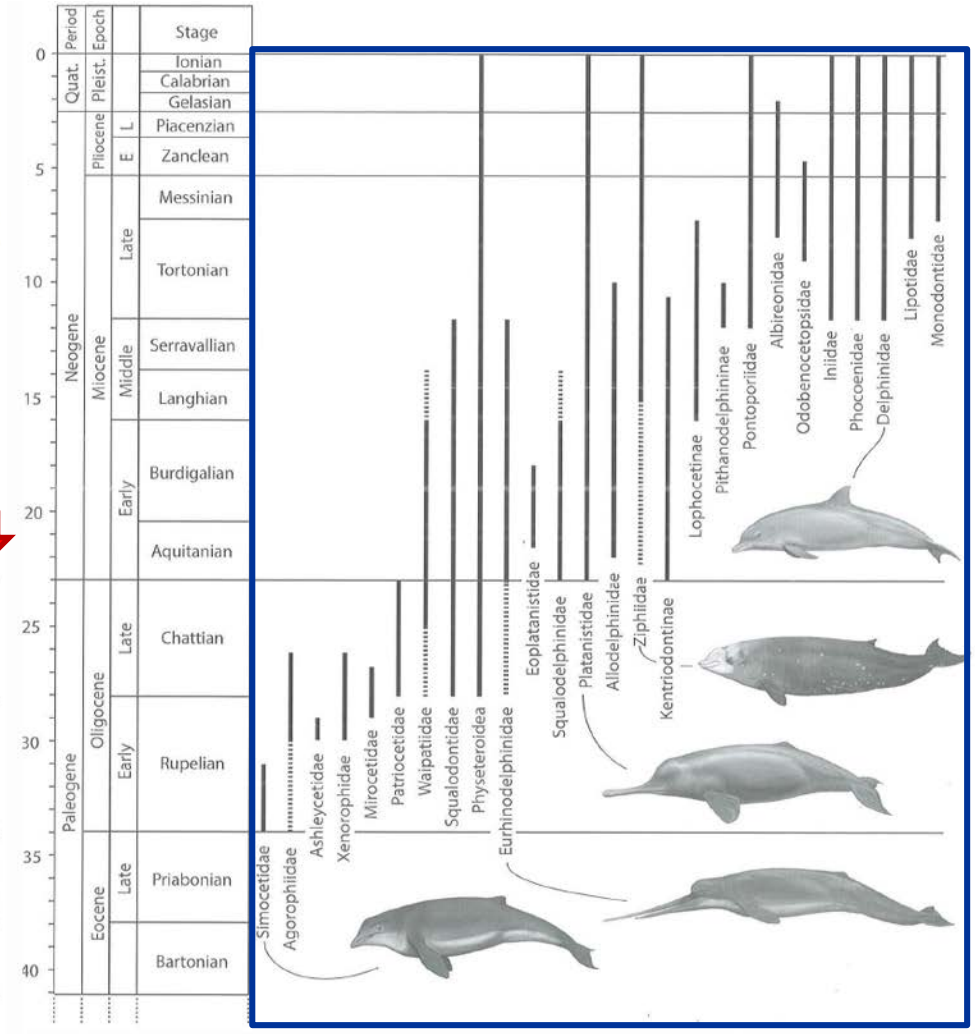
Mace Brown Museum of Natural History (Charleston, SC)

Photo: Matthew Campbell

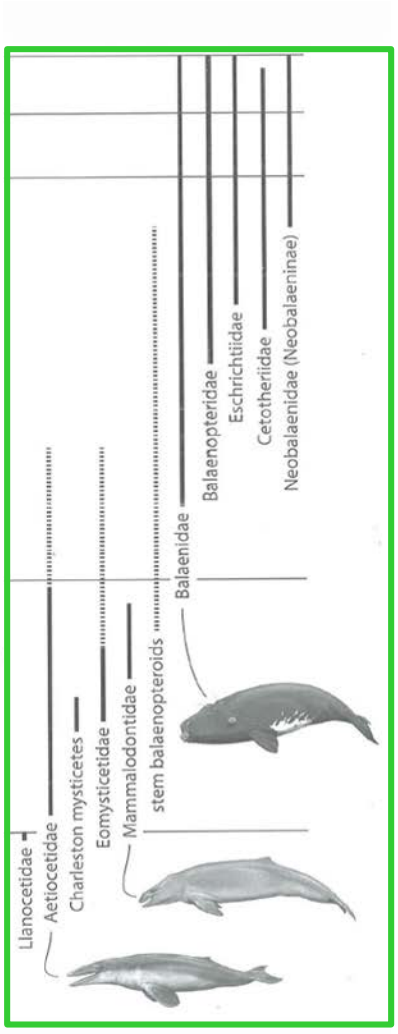
Eocene Archaeocetes



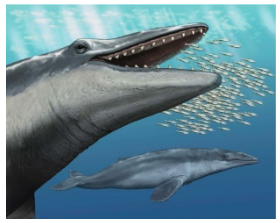




Odontocetes



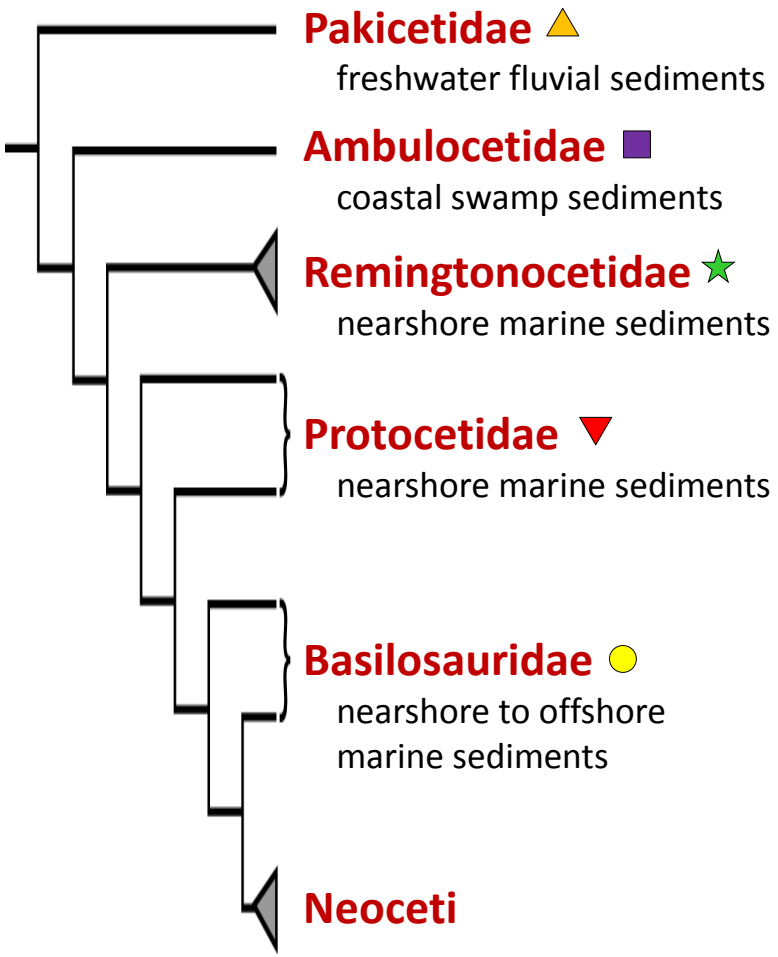
Mysticetes



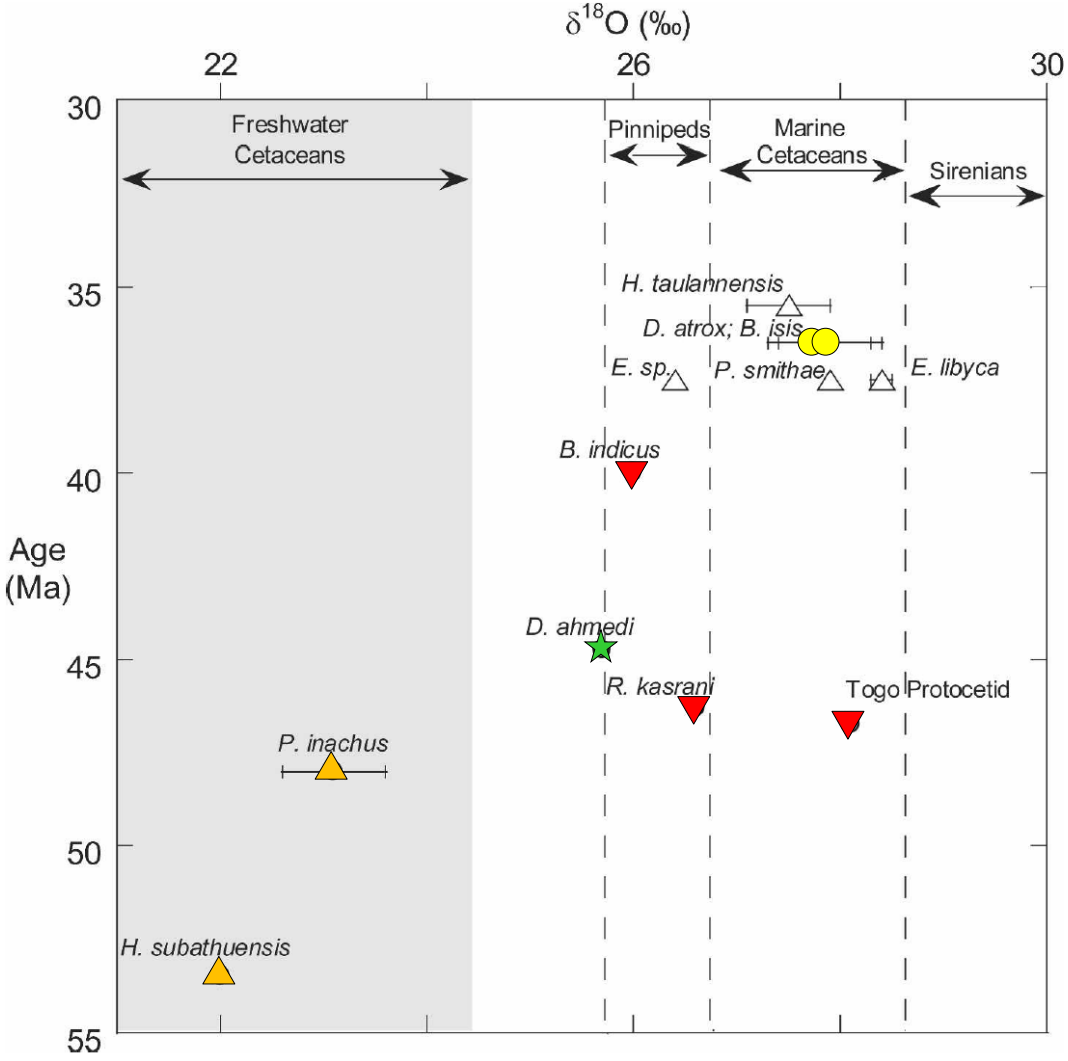
Marx et al. 2016

Paleoenvironments of Early Cetaceans

Depositional environments

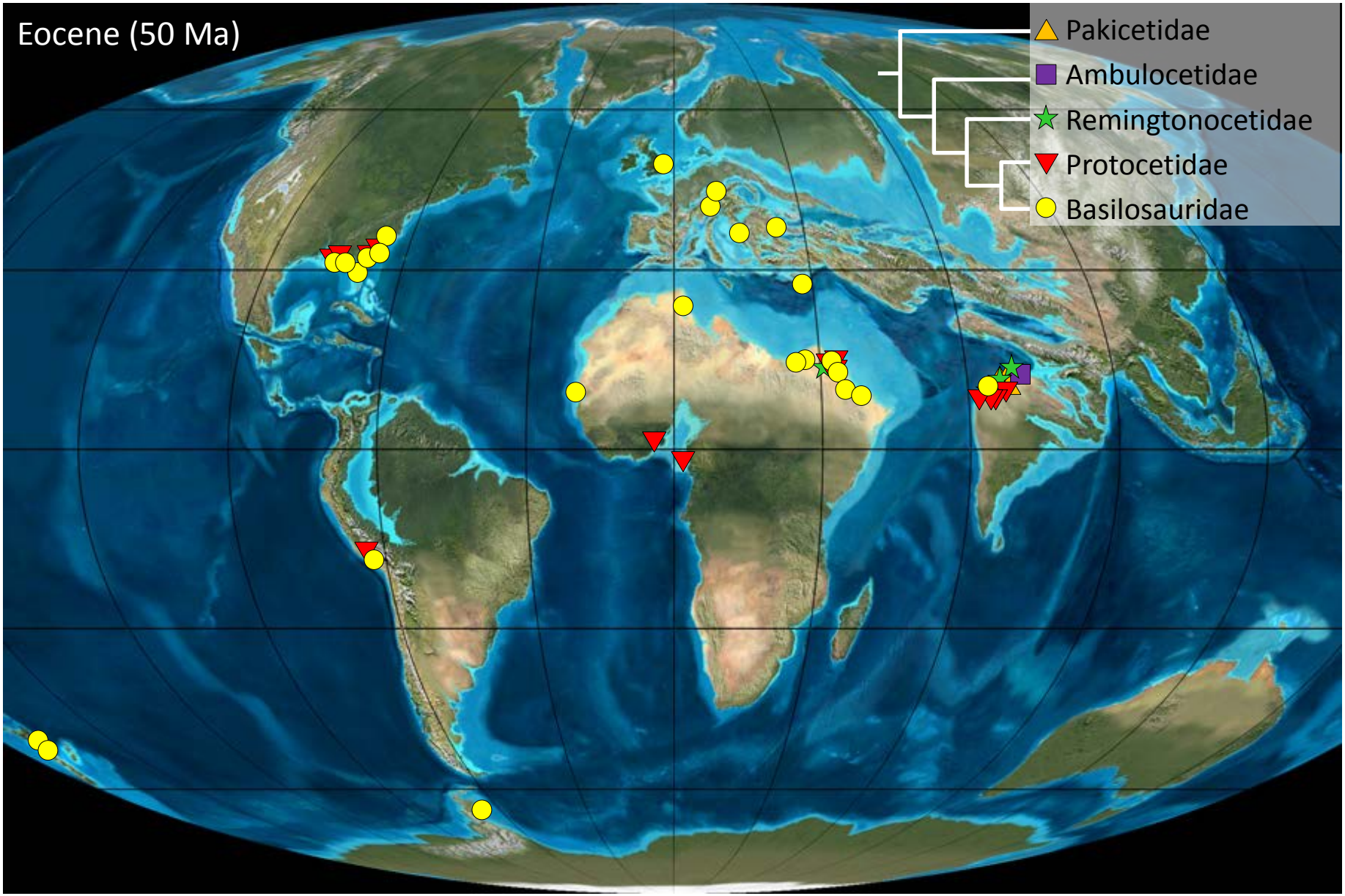


Stable isotope analyses

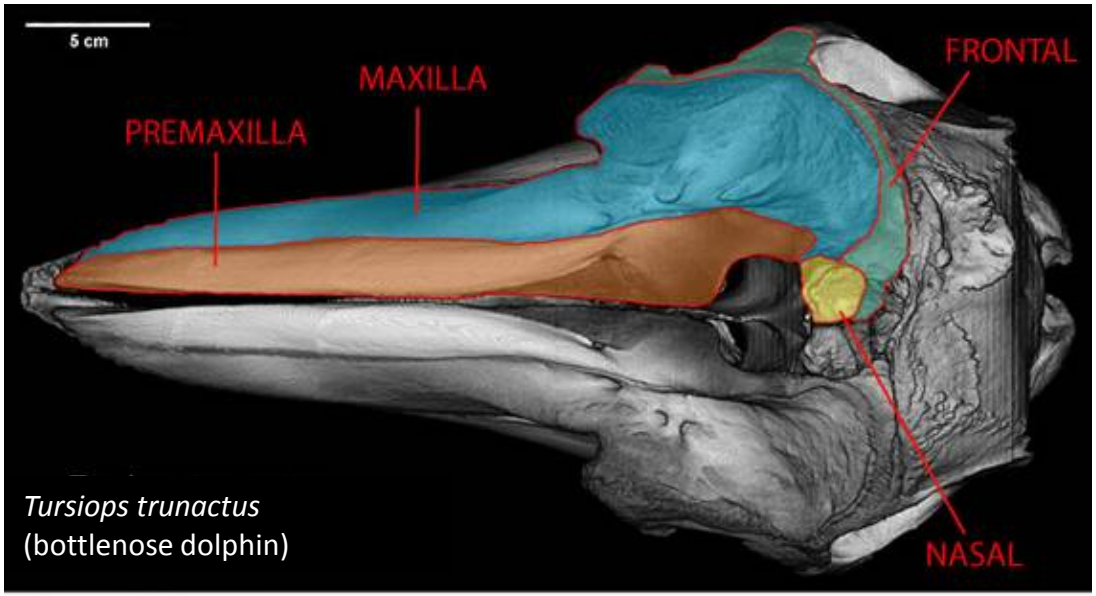


Clementz et al. 2006

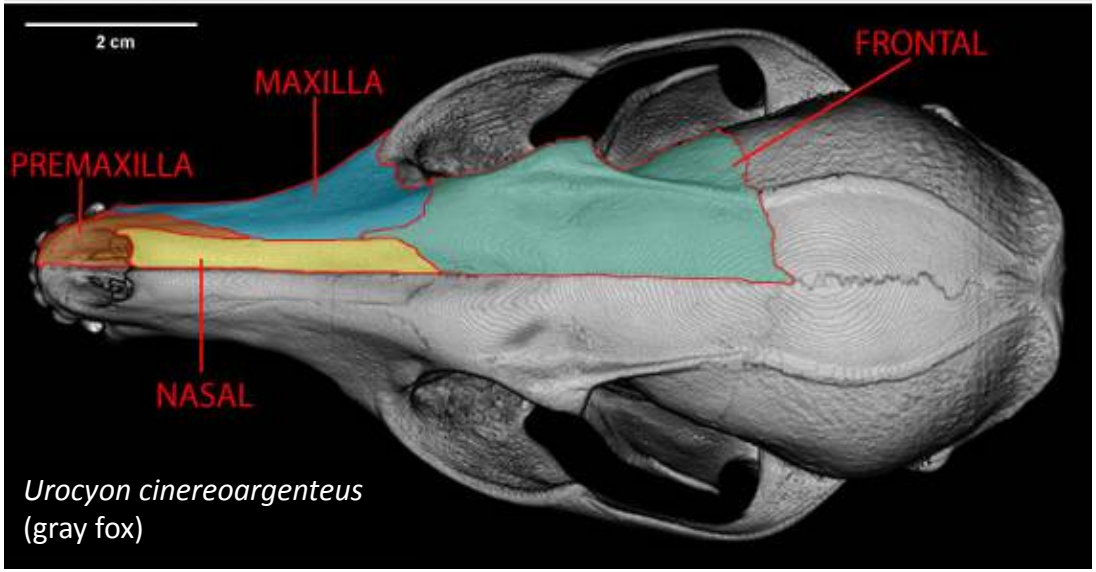
Biogeography of Early Cetaceans



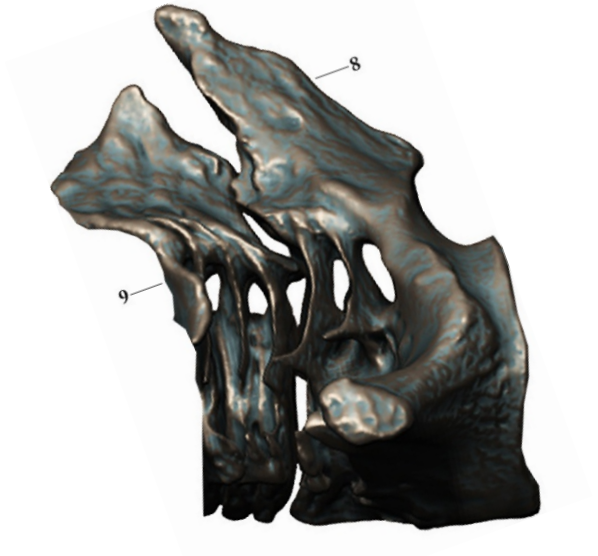
Comparative Anatomy of Cetaceans



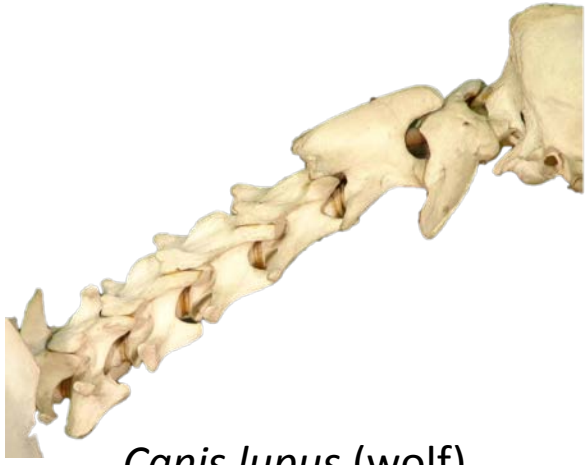
Tursiops trunactus
(bottlenose dolphin)



Urocyon cinereoargenteus
(gray fox)

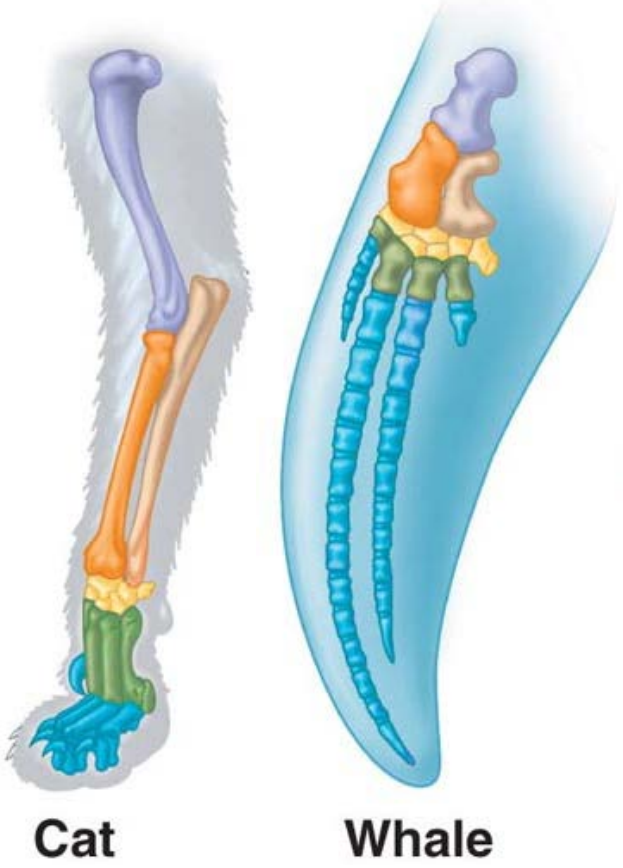


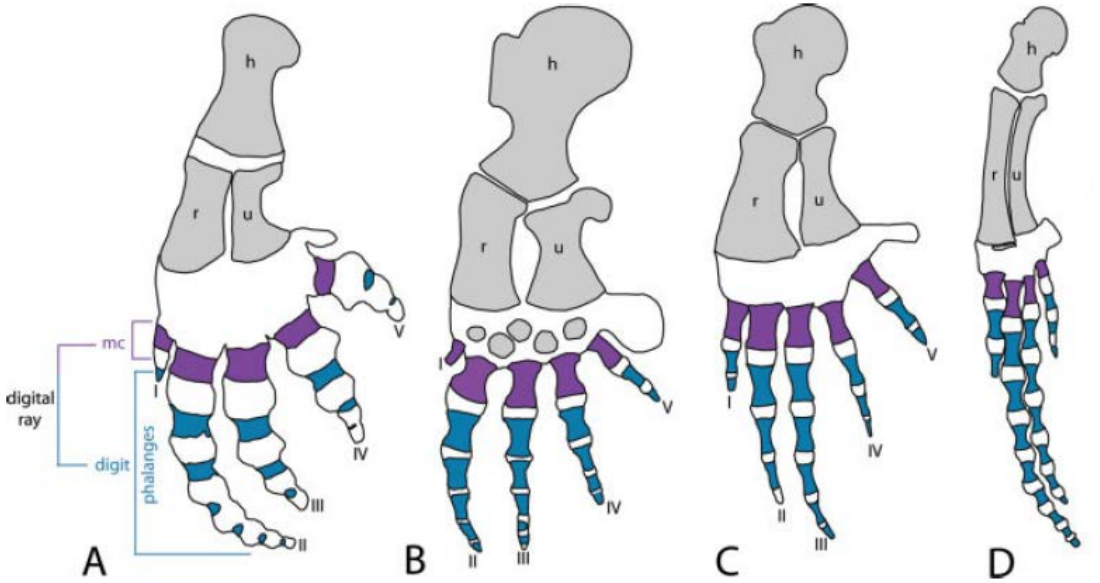
Orcinus orca (killer whale)
cervical vertebrae (C1-C7)



Canis lupus (wolf)
cervical vertebrae (C1-C7)

Comparative Anatomy of Cetaceans





Orcinus orca (killer whale)

Physeter macrocephalus (sperm whale)

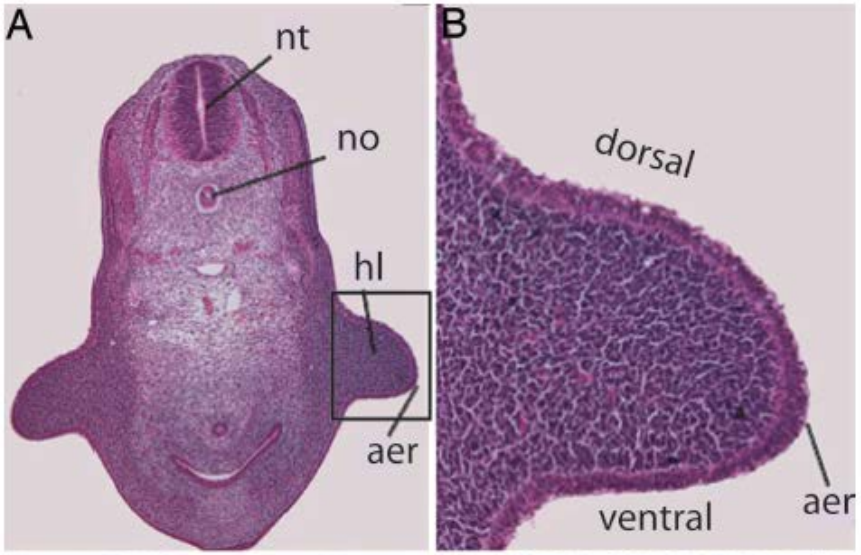
Eubalaena glacialis (N. Atlantic right whale)

Megaptera novaeangliae (humpback whale)

Cooper et al. 2007, Cooper 2009

Development of Hind Limbs in Cetaceans

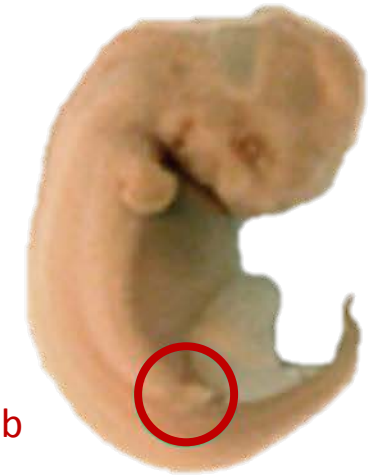
Stenella attenuata (pantropical spotted dolphin)



Carnegie Stage 12
LACM 94657

Carnegie Stage 13
LACM 94701

Hind limb buds



Carnegie Stage 16
LACM 94651

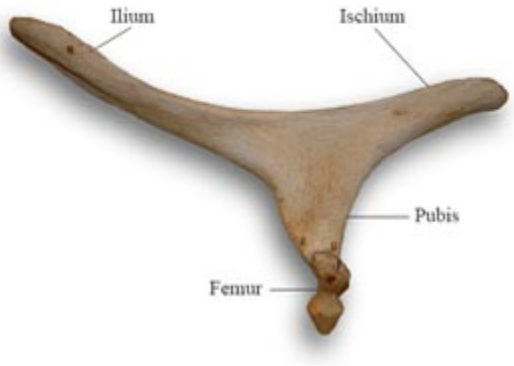
Carnegie Stage 17
LACM 94670

Thewissen et al. 2006, 2009

Development of Hind Limbs in Cetaceans

Eubalaena glacialis
(N. Atlantic right whale)

Balaenoptera physalus
(fin whale)



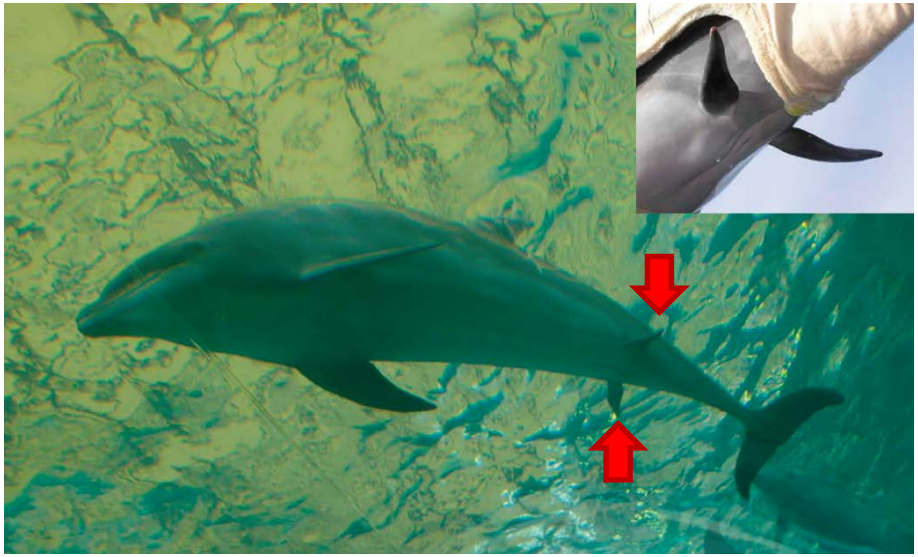
Orcinus orca
(killer whale)

Physeter macrocephalus
(sperm whale)

MARINE MAMMAL SCIENCE, 24(3): 743–745 (July 2008)

DOI: 10.1111/j.1748-7692.2008.00202.x

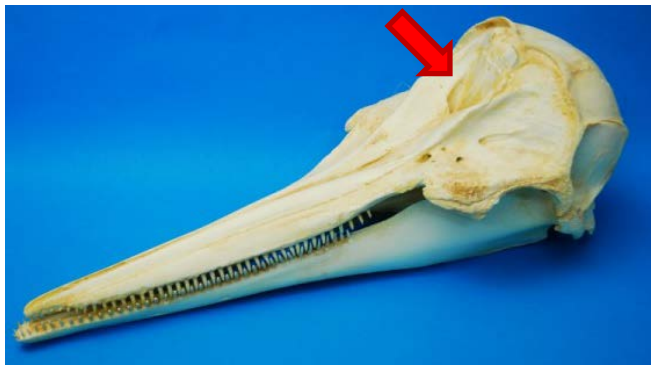
A BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)
WITH FIN-SHAPED HIND APPENDAGES

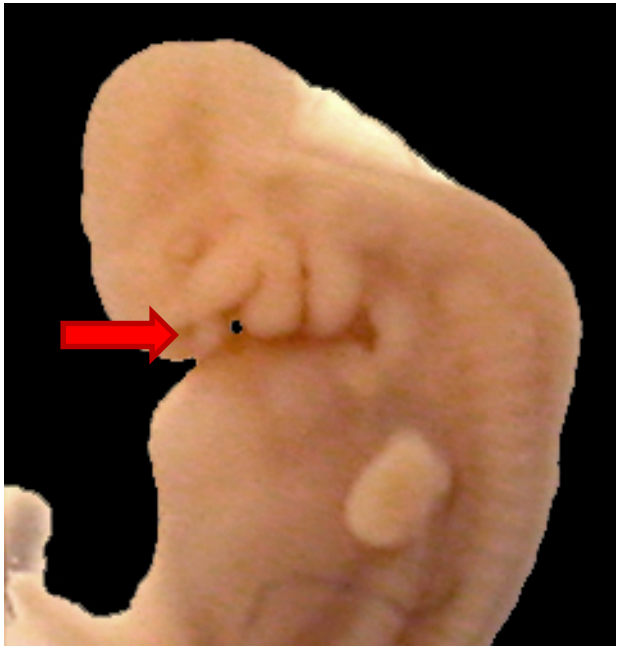


Ohsumi and Kato 2008

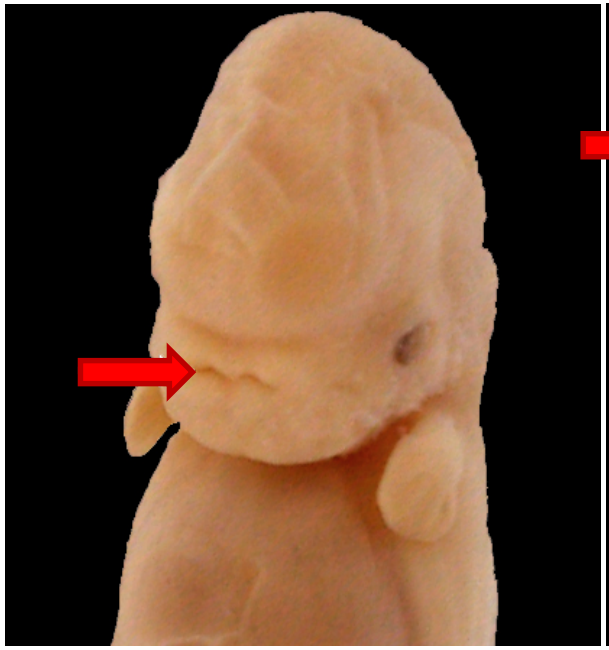
Development of Blowholes in Cetaceans

Stenella attenuata (pantropical spotted dolphin)

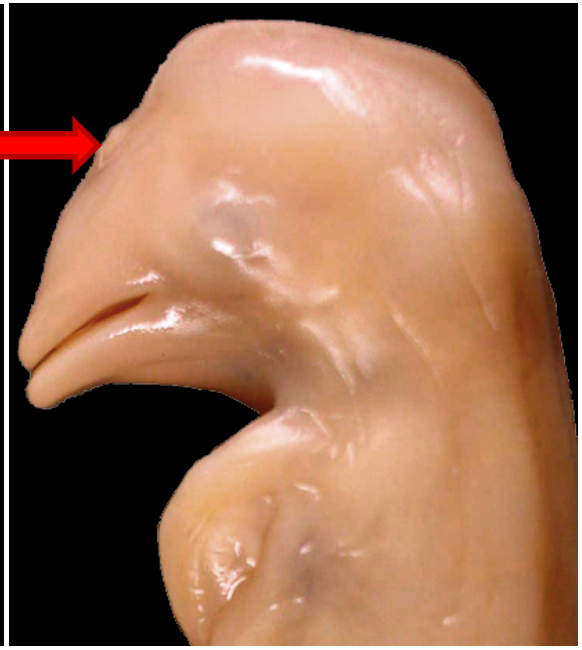




Carnegie Stage 14
LACM 94594



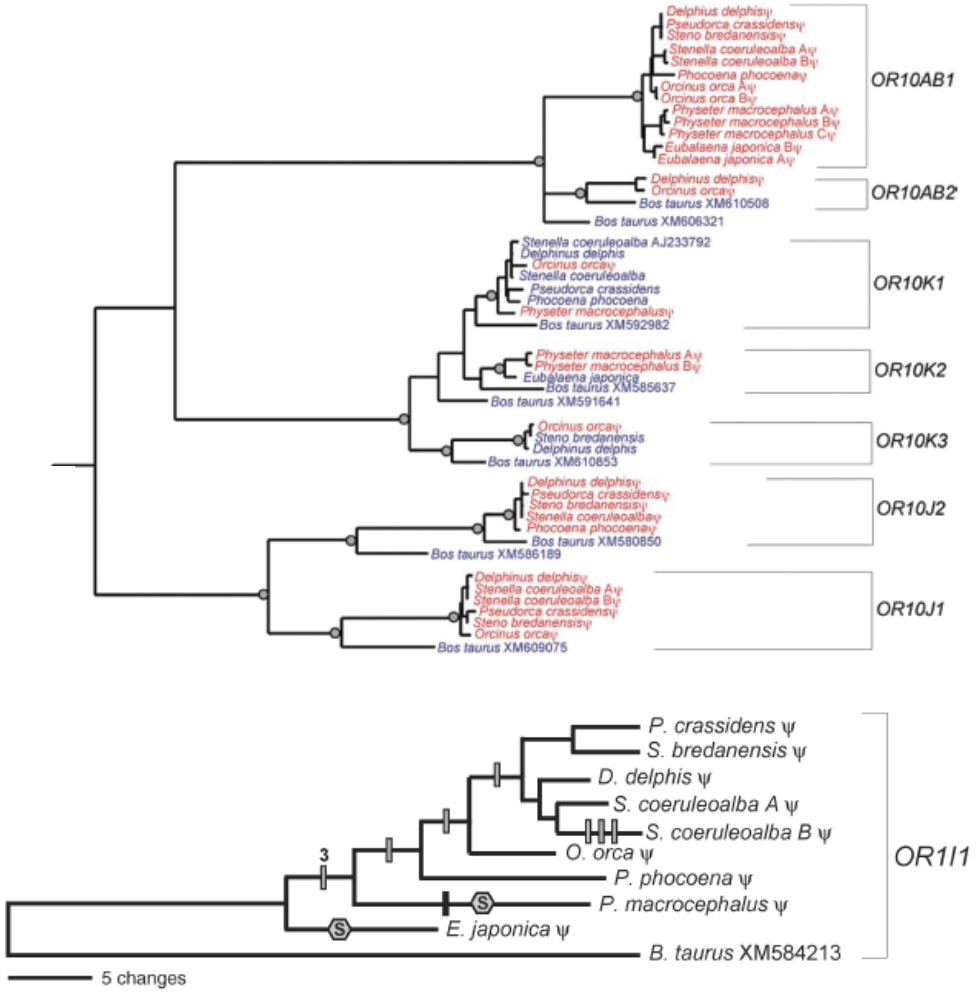
Carnegie Stage 17
LACM 94670



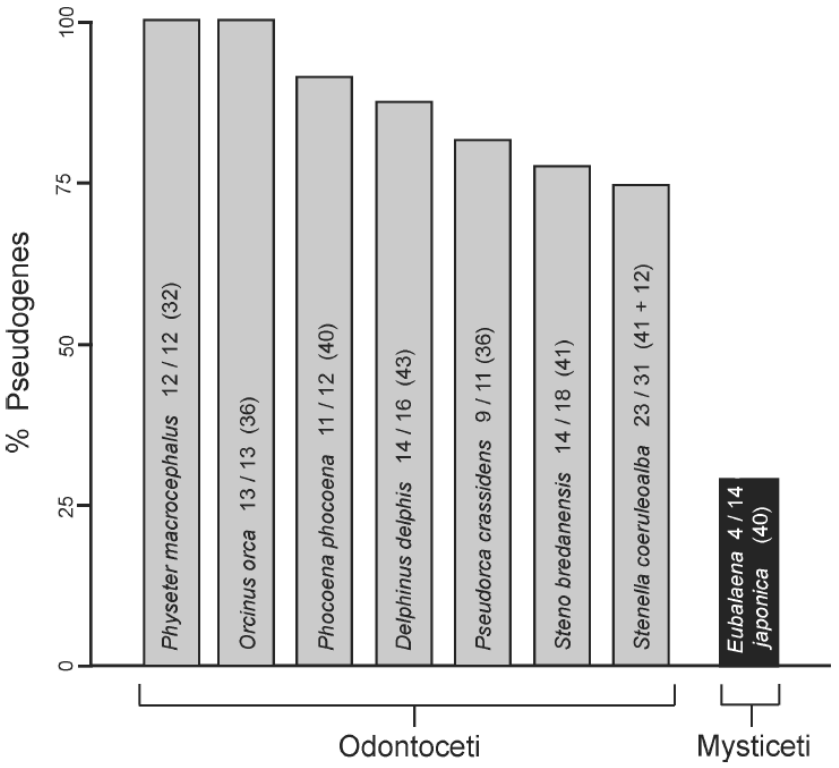
Fetus
LACM 94607

http://web.neomed.edu/web/anatomy/DLDD/interst/develop/blowhole/index.html

Genetics of Cetaceans



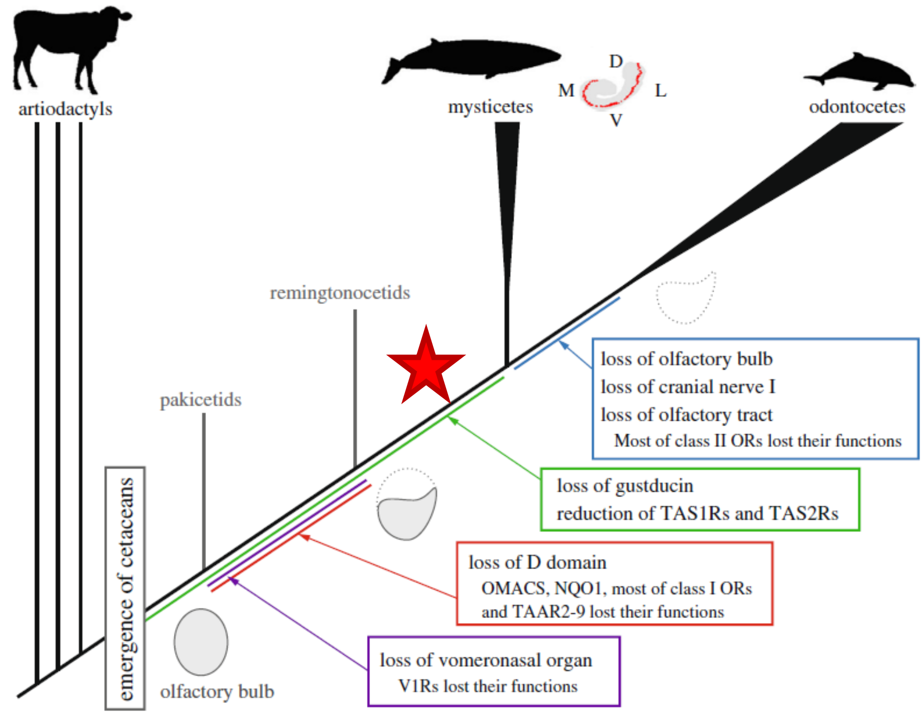
Olfactory receptor genes are detectable in cetacean genomes but most (~79%) have become **pseudogenes**



McGowen et al. 2008

Genetics of Cetaceans

- Massive reduction in no. of taste receptor genes (*TAS1R*, *TAS2R*)
- Pseudogenization mutations in *GNAT3* (α-subunit of gustducin) shared by odontocetes and mysticetes → loss of sweet, umami, and bitter sensation
- Findings suggest that gustatory ability was greatly reduced in common ancestor of Neoceti



Exon 6 of *GNAT3*:

```
Positions: 630, 640, 643, 650, 658, 659, 660, 670, 680, 682, 690, 700, 710, 720

homSapGNAT3-GRCh37 (Human)             AAAGAAGTGGATTCACTGCTTTGAAGGAGTTACATGCATTATATTTTGT GCTGCACTTAGTGCCTATGACATGGTCCTCGTGGAAGACGAAGAAGTG
musMusGNAT3-GRCm38 (Mouse)             AAAAAAATGGATCCACTGCTTTGAAGGAGTCACCTGCATTATATTTTGC GCAGCGCTAAGTGCCTATGACATGGTGCTTGTAGAAGATGAGGAGGTG
bosTauGNAT3-NM_001109982.1 (Cow)       AAAGAAATGGATTCACTGCTTTGAAGGAGTTACATGCATTATATTTTGT GCTGCACTCAGTGCCTATGACATGGTTCTGGTGGAAGATGAAGAAGTG
hipAmpGNAT3 (Hippopotamus)             AAAGAAATGGATTCACTGCTTTGAAGGAGTTACATGCATTATATTTTGT GCTGCACTCAGTGCCTATGACATGGTCCTGGTGGAAGATGAAGAAGTG
balBonGNAT3-KUjira_1.0 (Minke whale)   AAAGAAATGGATTCACTAC-TTGAAGGAGTTACATGAATTATATTTTGT GCTGCACTC-GTGCCTATGACATGGTCTTGGTGGAAGATGAAGAAGTG
balBonGNAT3-hap1 (Minke whale)         AAAGAAATGGATTCACTAC-TTGAAGGAGTTACATGAATTATATTTTGT GCTGCACTC-GTGCCTATGACATGGTCTTGGTGGAAGATGAAGAAGTG
balBonGNAT3-hap2 (Minke whale)         AAAGAAATGGATTCACTAC-TTGAAGGAGTTACATGAATTATATTTTGT GCTGCACTCAGTGCCTATGACATGGTCTTGGTGGAAGATGAAGAAGTG
balBorGNAT3 (Sei whale)                AAAGAAATGGATTCACTAC-TTGAAGGAGTTACATGAATTATATTTTGT GCTGCACTCAGTGCCTATGACATGGTCTTGGTGGAAGATGAAGAAGTG
turTruGNAT3-Ttru_1.4 (Bottlenose dolphin) AAAGAAATGGATTCCCTCC-TTGAAGGAGTTACATGAATTATATTTTGT GCTGCAGTCAGTGCCTATGATATGCTCTTGGTGGAAGATGAAGAAGTG
phoDalGNAT3 (Dall's porpoise)          AAAGAAATGGATTCACTCC-TTGAAGGAGTTACATGAATTATATTTTGT GCTGCACTCAGTGCCTATGACATGGTCTTGGTGGAAGATGAAG---TG
                                       *** ** ***** * ** * ********** ** ** *********** *** ** ** * *********** *** * * ** ***** ** * **
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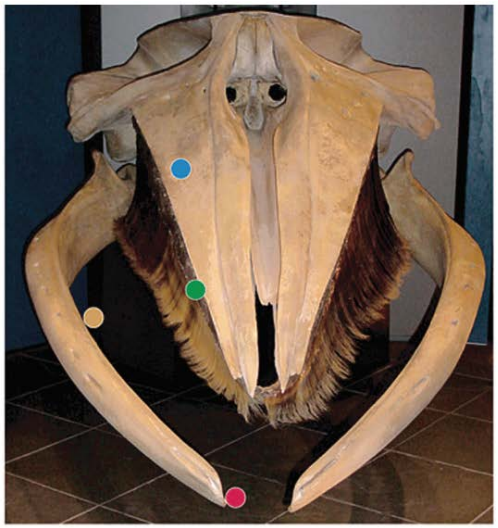
Kishida et al. 2015

Genetics of Cetaceans



Balaenoptera acutorostrata
(minke whale, modern)

Aetiocetus weltoni
(24-28 Ma)

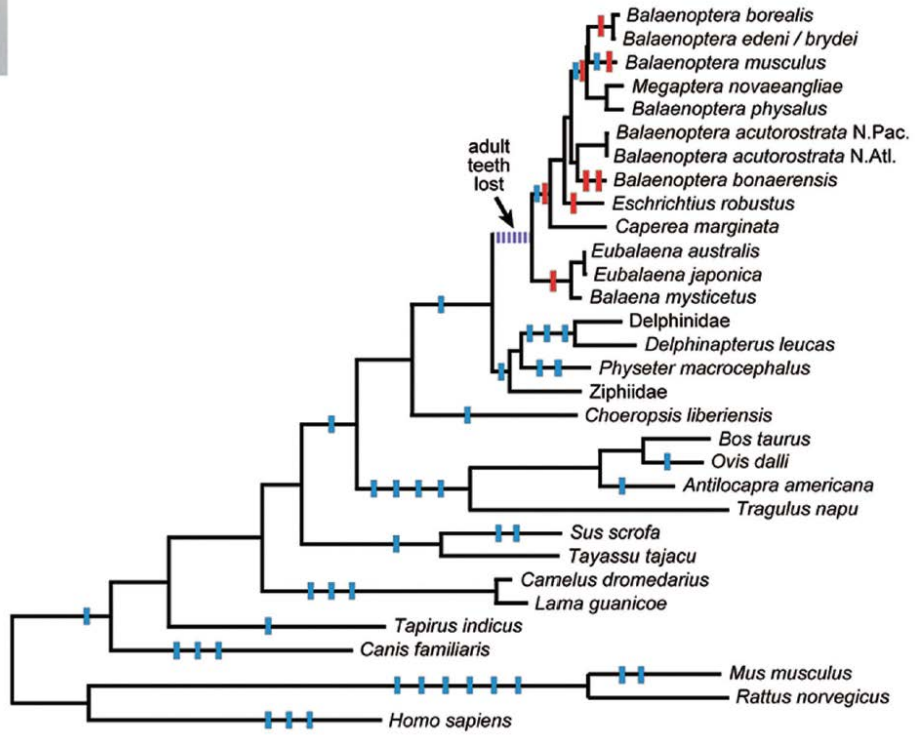
AMBN

```
B.bor.  ATGCCCCCC-AATCCAGCC..AACCCCCTCCCTGTGCCGCAGGCCAACCCA
B.mus.  ATGCCCCCC-AATCCAGCC..AAGACCCCCC-TGTGCCAGAGGCCAACCCA
E.rob.  ATGCCCCCC-AATCCAGCC..AACCCCCCCC-TGTGCCGCAGGCC-ACCCA
E.jap.  ATGCCCCCCCAATCCAGCC..AAGACCCCCC-TGTGCCAGAGGCCCACCCA
B.mys.  ATGCCCCCCCAATCCAGCC..AAGACCCCCC-TGTGCCAGAGGCCAACCCA
S.scr.  ATGCCCCCC-AACTCAGCC..AAGGCTCTCC-AGTGGCGGAGGCCAACACA
```

ENAM

```
B.bor.  CACCTTTTAAGGAAG..AGGATGTGTTTACTACCCTGACTATA
B.mus.  CACCTTT-AAGGAAG..AGGATGTGTTTACTACCCTGACTATA
E.rob.  CACCTTTTAAGGAAG..AGGACGCG-TTACTAC------TATA
E.jap.  CACCTTTTAAGGAAG..AGGACGTGTTTACTACCCTGACTATA
B.mys.  CACCTTTTAAGGAAG..AGGACGTGTTTACTACCCTGACTATA
S.scr.  CACCTTTTAAAGAAG..AGTACATGTTTACTACCCTGACTATA
```

- Enamel-specific genes (e.g., AMBN, ENAM) are present in modern toothless mysticetes, but have degraded into pseudogenes



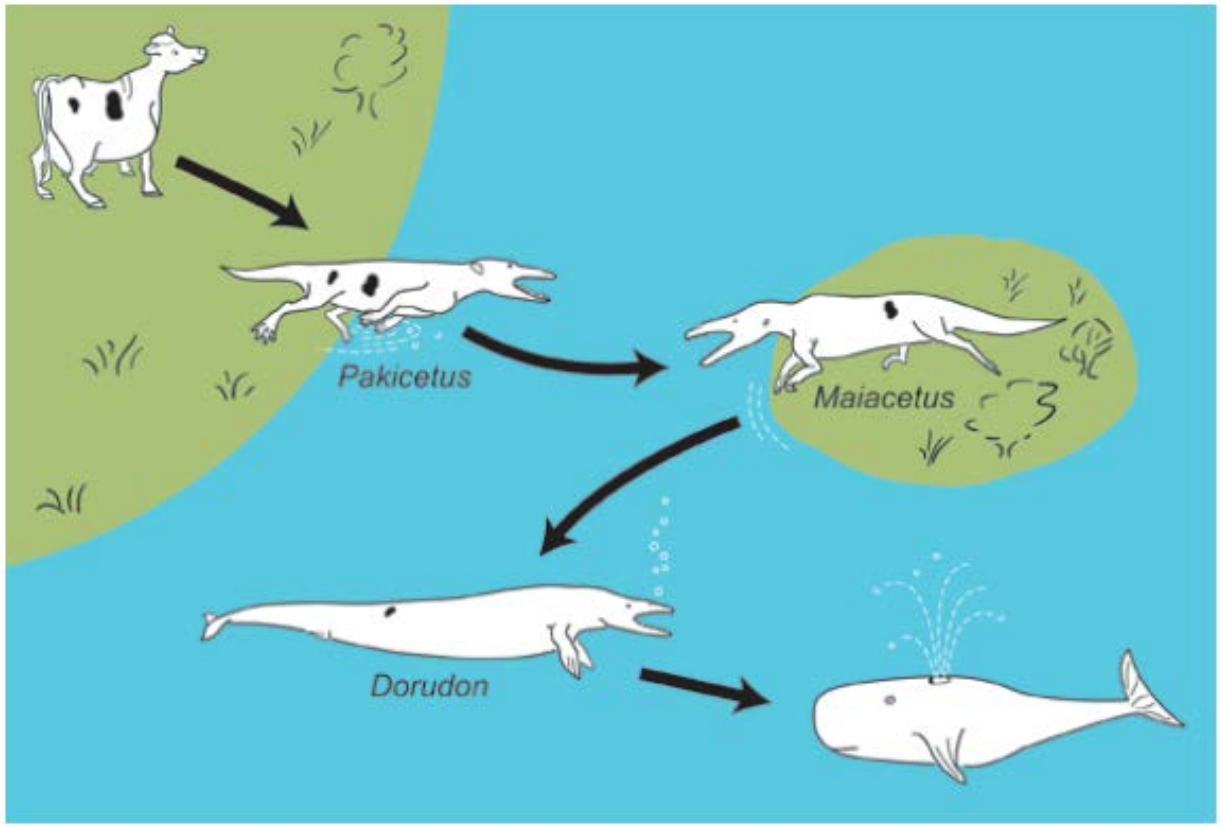
Deméré et al. 2008

Summary

- The evidence for the evolution of cetaceans from terrestrial ancestors comes from many different fields…
  - Fossil cetaceans with intermediate anatomies appear when and where we expect to find them
  - Comparative anatomy and ontogeny demonstrate striking similarities between cetaceans and terrestrial mammals
  - Genetics allows the molecular basis for anatomical/physiological changes to be studied at incredible levels of detail
- Together, these independent lines of evidence converge on a single explanation…

Summary

- Though ***there is still much to learn***, the origin of cetaceans has gone from one of evolution's biggest mysteries to one of its most shining examples



Gingerich 2012; artwork by John Klausmeyer