Lost in transition: from teeth to baleen

Annalisa Berta
Department of Biology
San Diego State University
San Diego, CA 92182

SAN DIEGO STATE UNIVERSITY

Research Questions:

1. What was the ancestral feeding strategy in baleen whales?

    - Biting, suction, filter

2. When and how did tooth loss occur and baleen evolve?

Outline

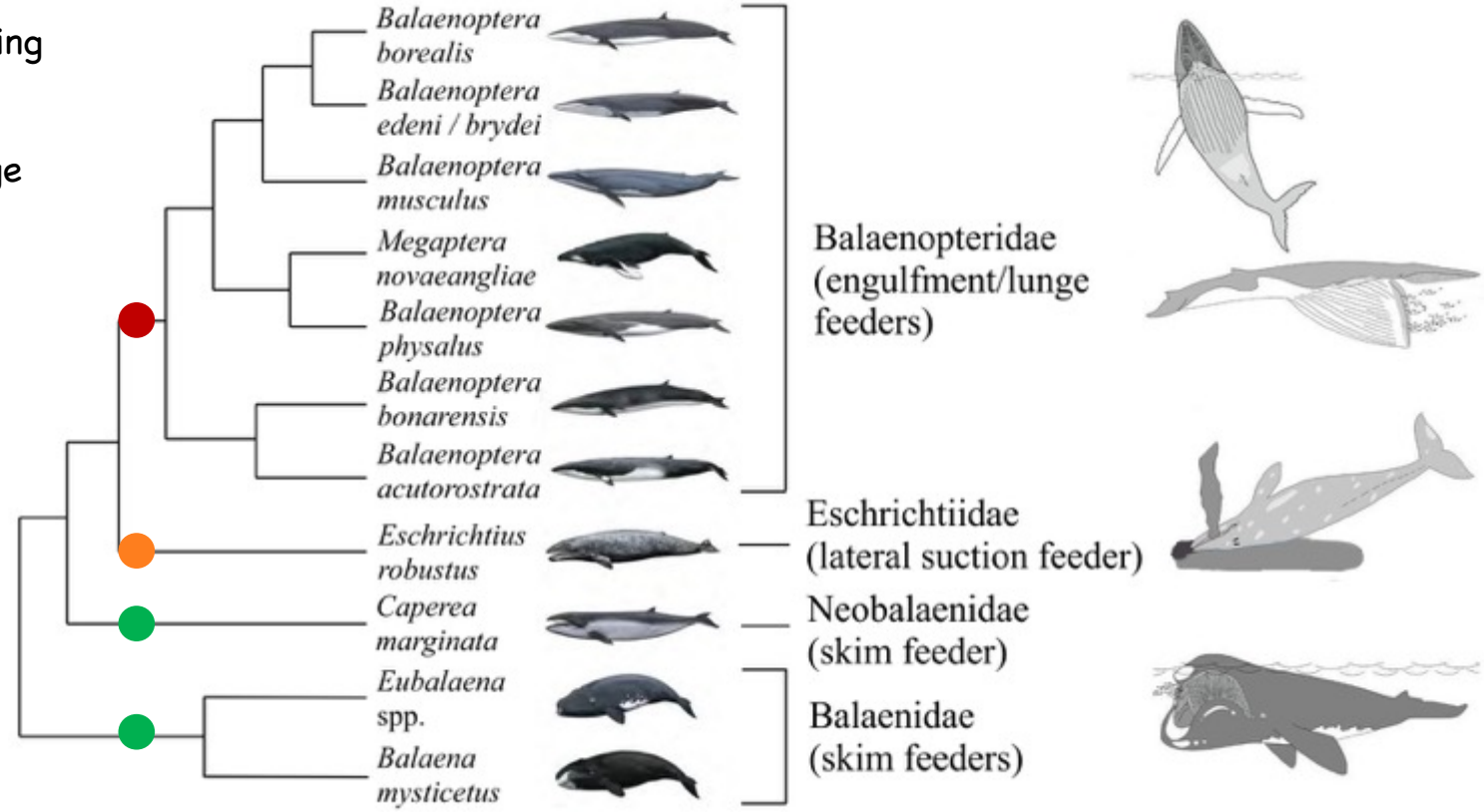
- Feeding strategies in living baleen whales

- Evidence for teeth and baleen
    - anatomy of modern whales and fossils
      baleen and blood supply
    - tooth genes
    - developmental and growth of skull
- Integration: Feeding in an Evolutionary Framework and Tooth to Baleen Transition

Modern mysticete diversity and feeding types

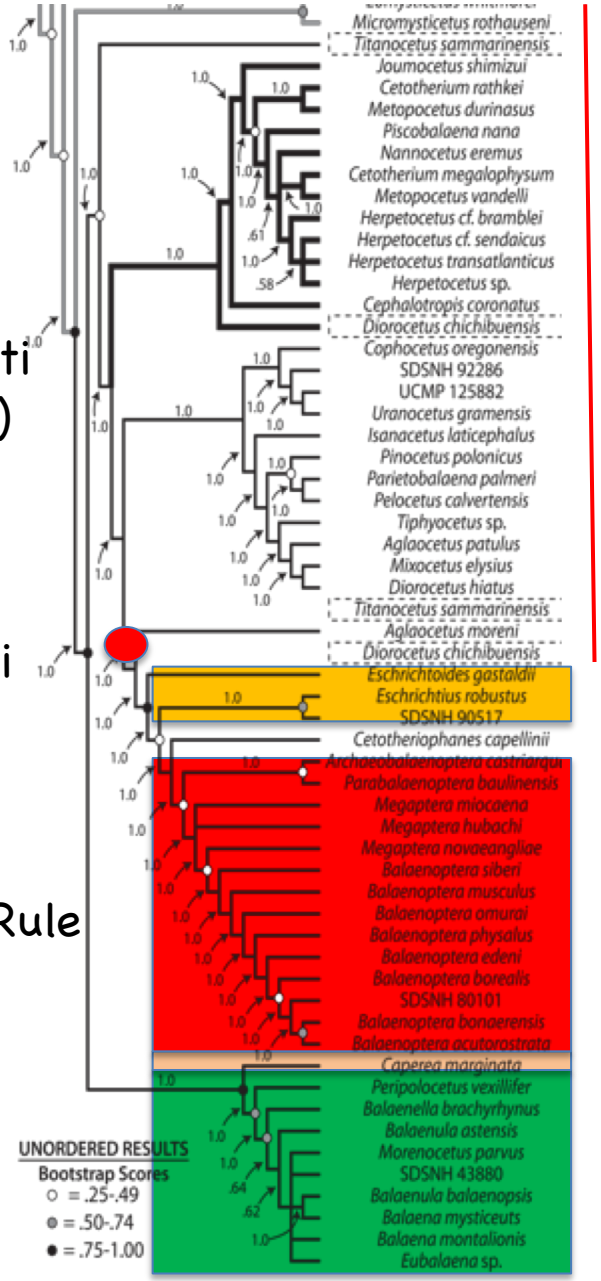
- Skim filter feeding
- Lateral suction filter feeding
- Engulfment/lunge filter feeding

14 spp. in
4 families



Modified from Gatesy et al., 2013

Preliminary Results: Mysticete Phylogeny



STEM Mysticeti (in part)

CROWN Mysticeti

Majority Rule

Cetotheriidae†

Eschrichtiidae

Balaenopteridae

Neobalaenidae

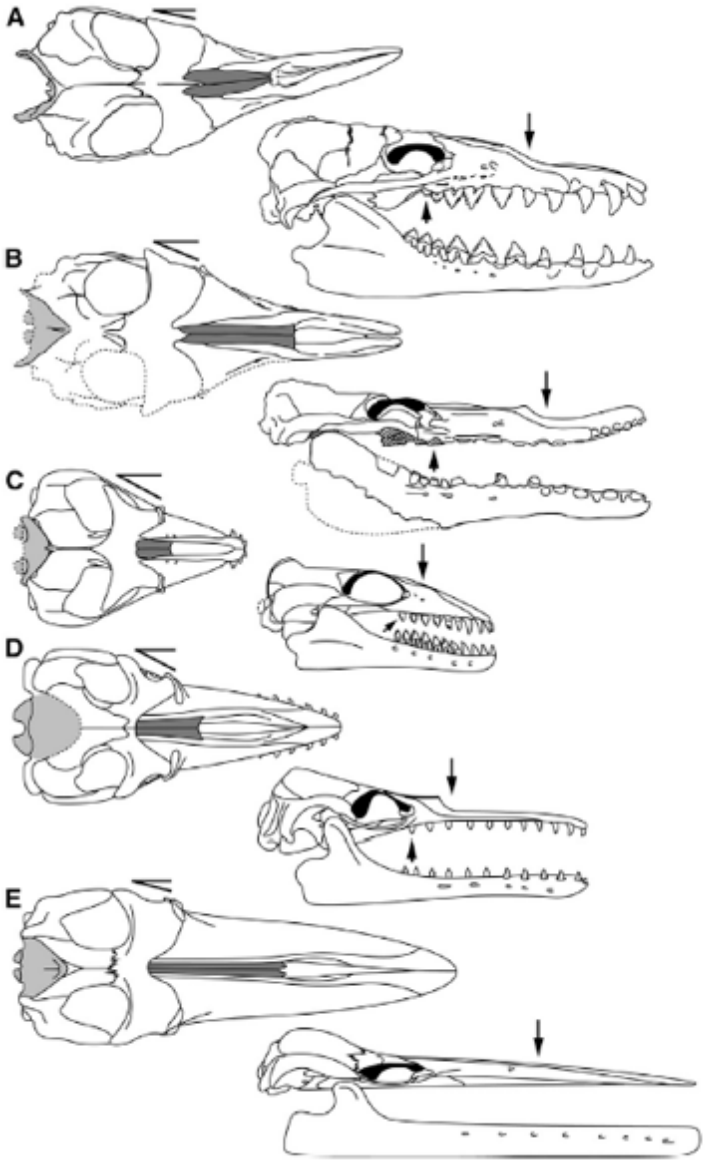
Balaenidae

TOTAL EVIDENCE

53 fossil spp.

Ekdale, El Adli, Deméré and Berta, in prep.

Feeding in Fossil Mysticetes



Archaeocete
Basilosaurus
biting

Mystacodon
suction

Janjucetus
biting

Aetiocetus
biting + filter

Eomysticetus
filter

- Common ancestor mysticetes and odontocetes: archaeocetes

- Earliest baleen whales

(36 Ma) 5 new fossils in last 2 years!

(No. and So. Pacific, So. Atlantic)

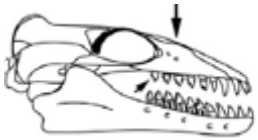
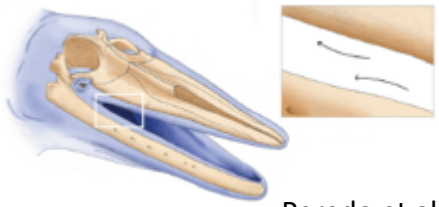
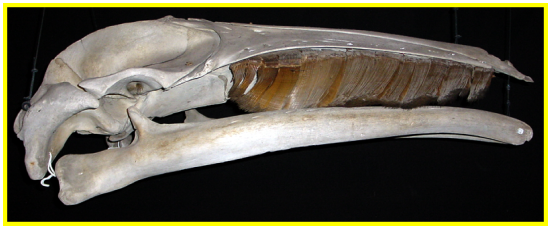
vary few-many teeth

- Feeding Hypotheses: Ancestrally, were they biters, suction, or filter feeders?

Lambert et al., 2017

Current Hypotheses

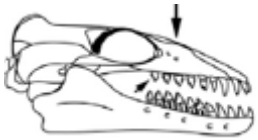
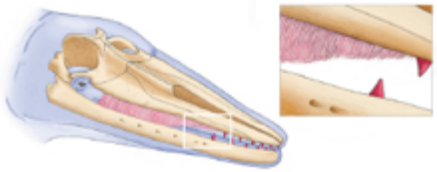
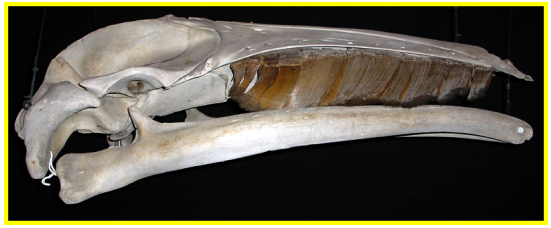
- Teeth to Baleen Transition:

Peredo et al., 2017

Teeth -> no teeth -> baleen only

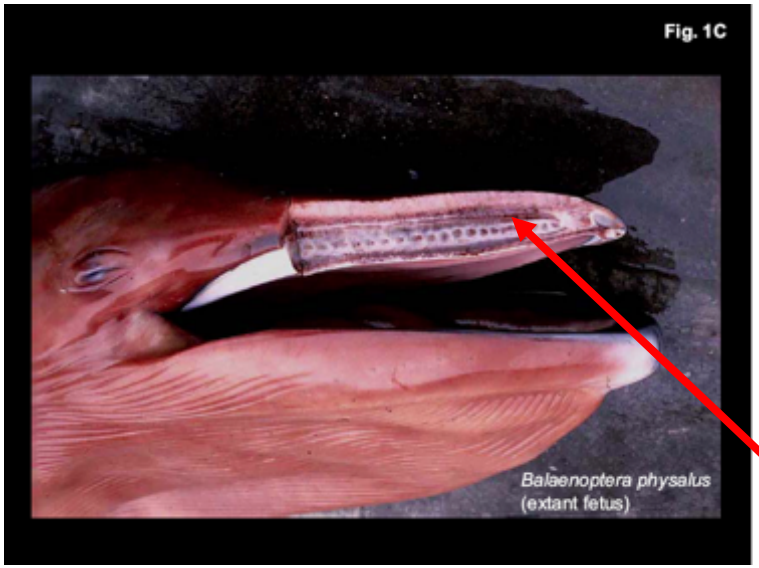
or

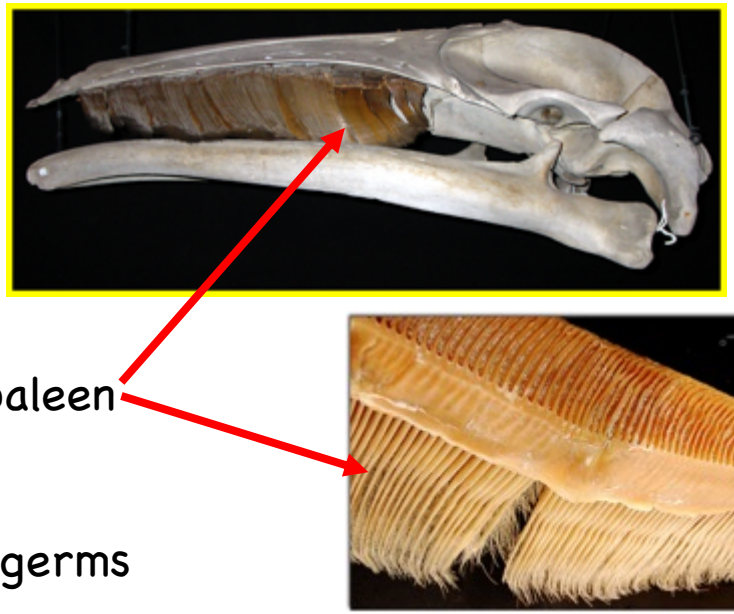




Peredo et al., 2017

Teeth -> teeth + baleen-> baleen only

Transition from teeth to baleen in modern mysticete whales

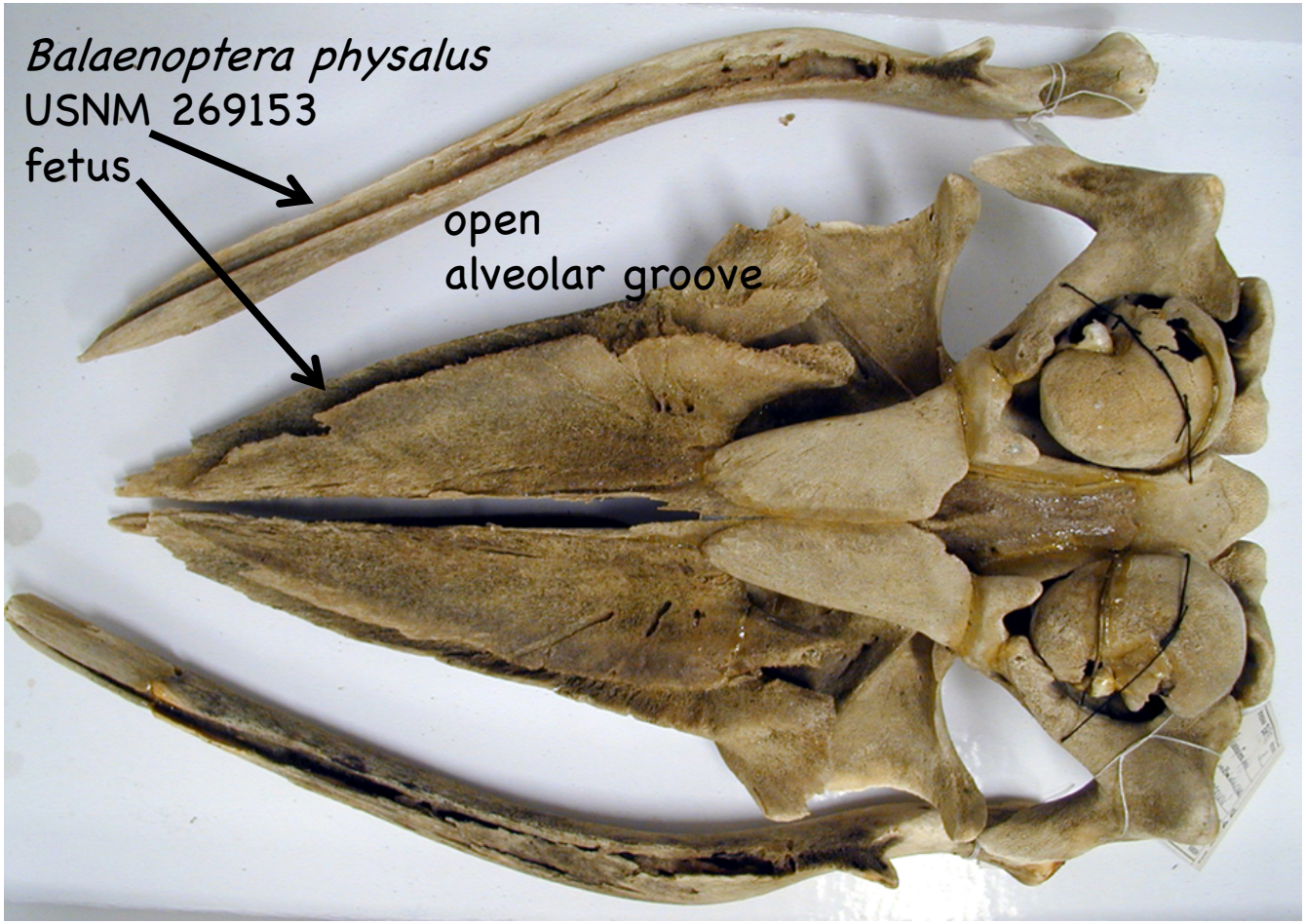




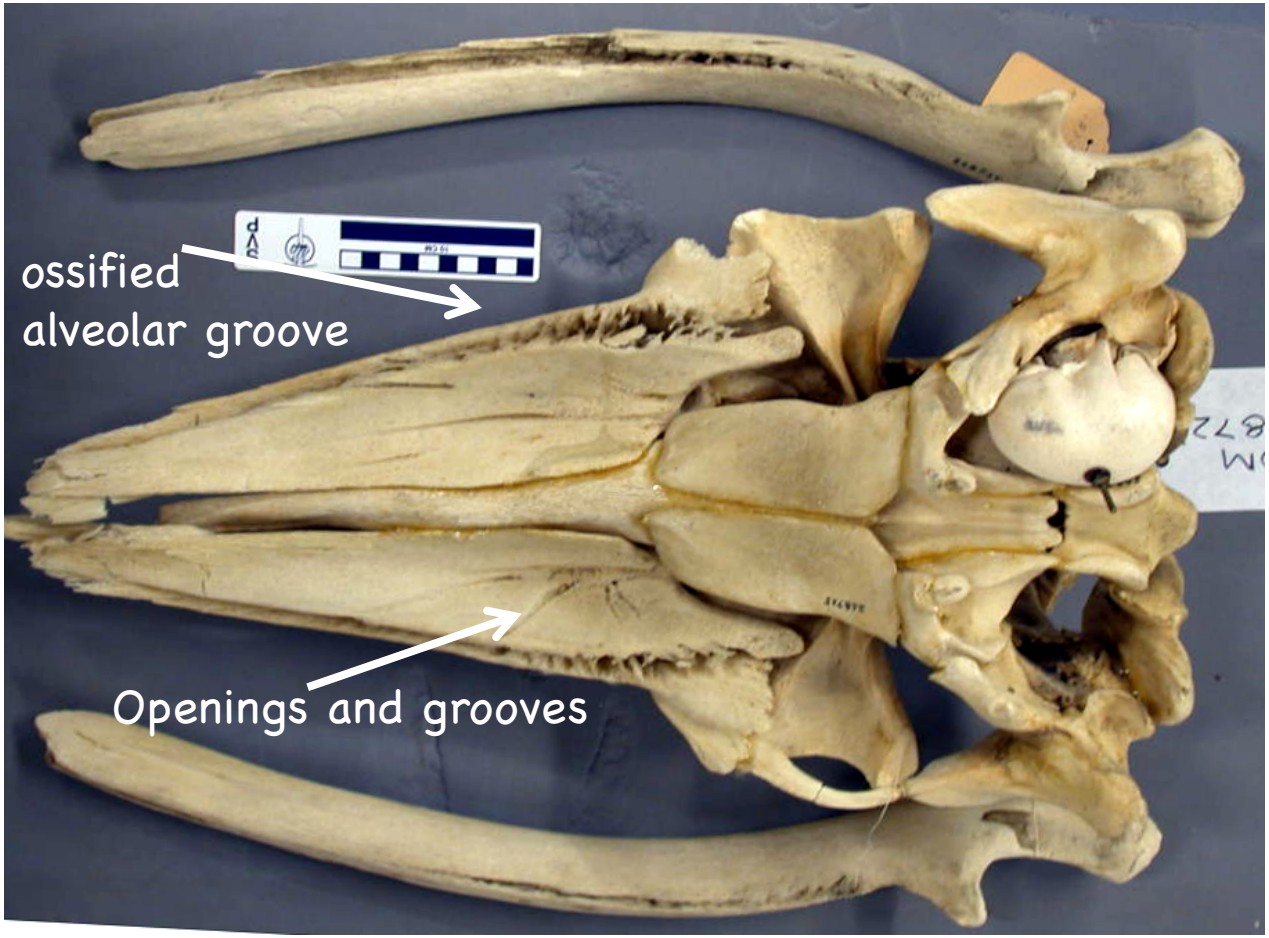
- baleen whales develop teeth that are resorbed before birth
- adult baleen whales lack teeth and possess baleen employed in filter feeding
- hypothesis for origin of filter feeding: teeth, teeth + baleen, baleen only

Deméré, McGowen, Berta and Gatesy 2008

Evidence for teeth- open alveolar groove

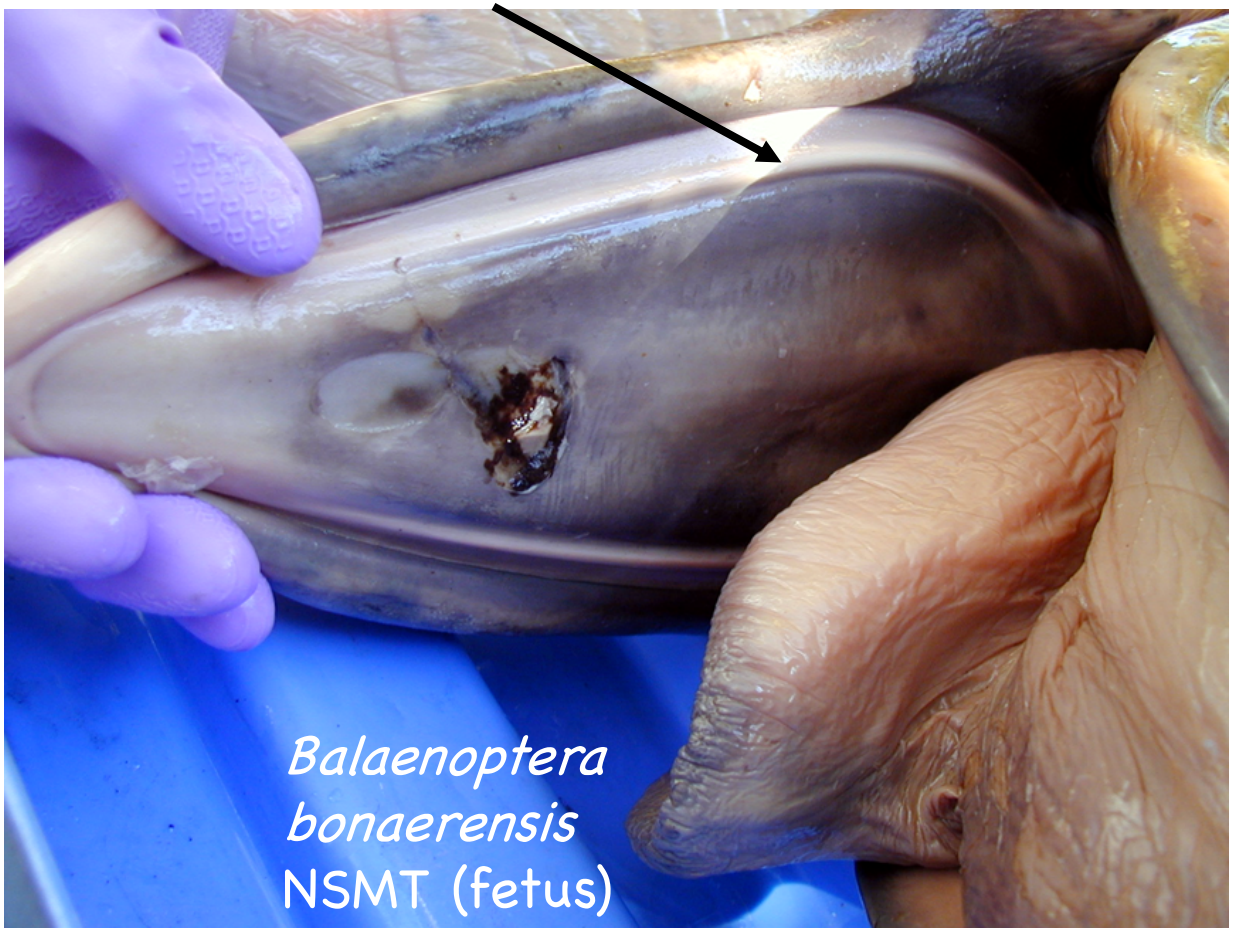


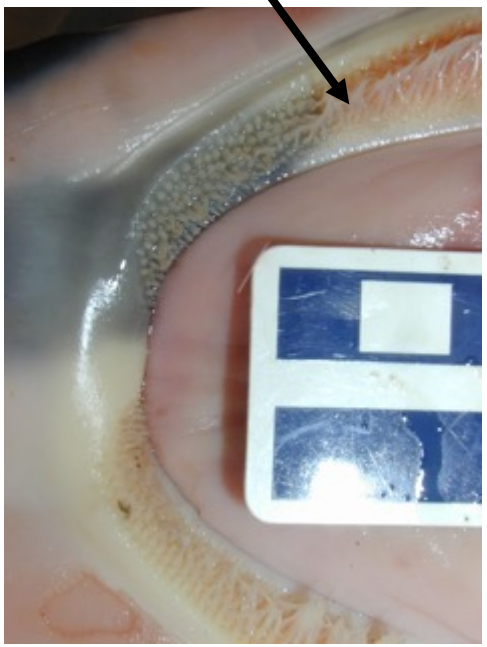
Evidence for teeth- ossified alveolar groove



Balaenoptera physalus – USNM 268925, fetus

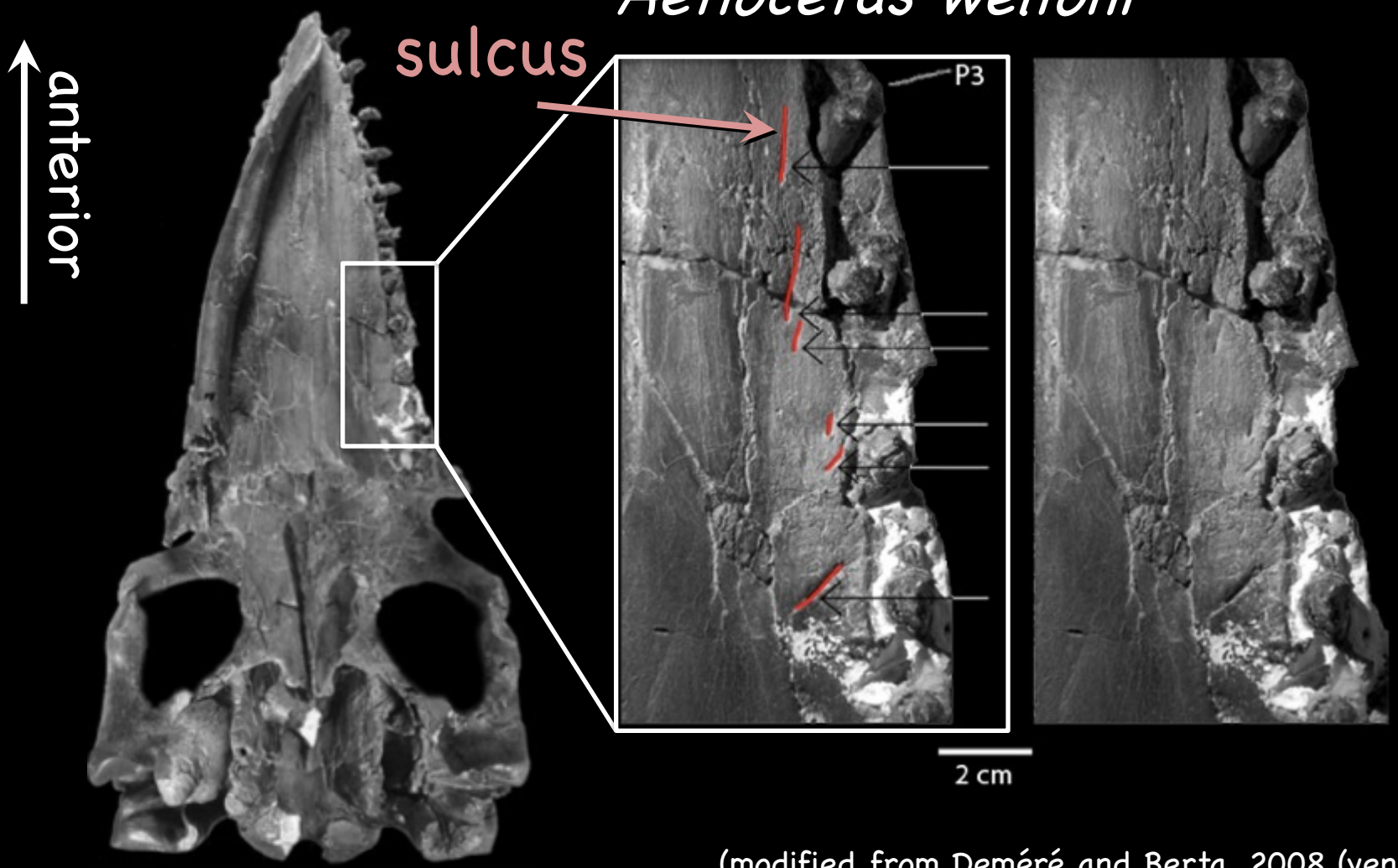
Baleen Development





Fossil Evidence for baleen-Stem Toothed Mysticete

Aetiocetus weltoni



24-28 Ma

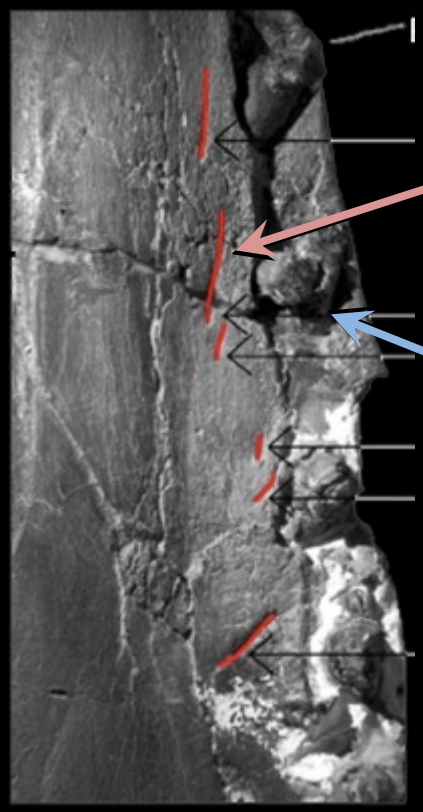
(modified from Deméré and Berta, 2008 (ventral view)

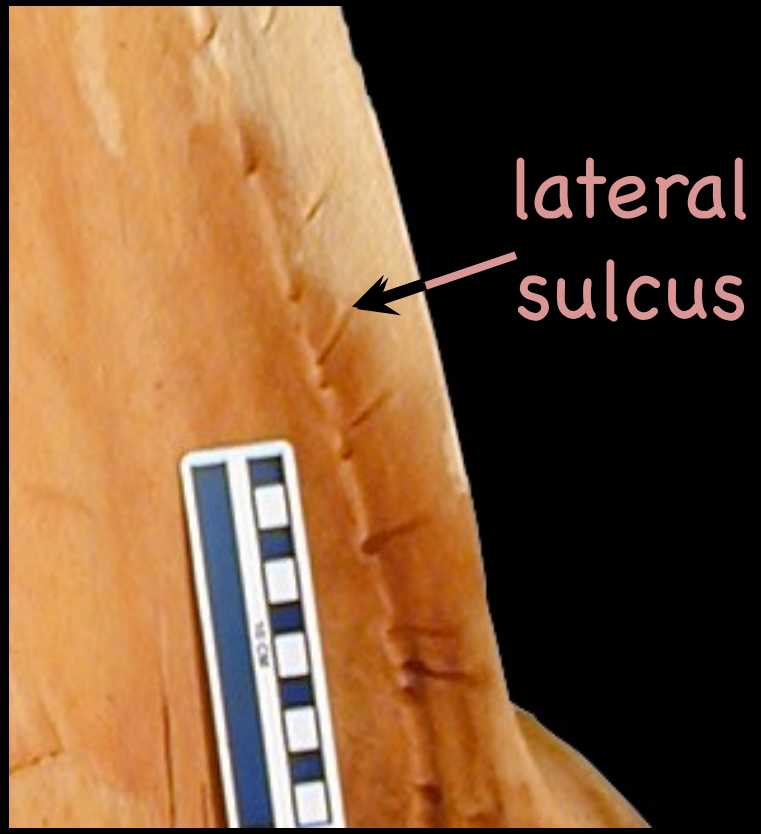
Evidence for baleen in fossil and and extant whales

Extinct *Aetiocetus weltoni*

Extant minke whale

anterior





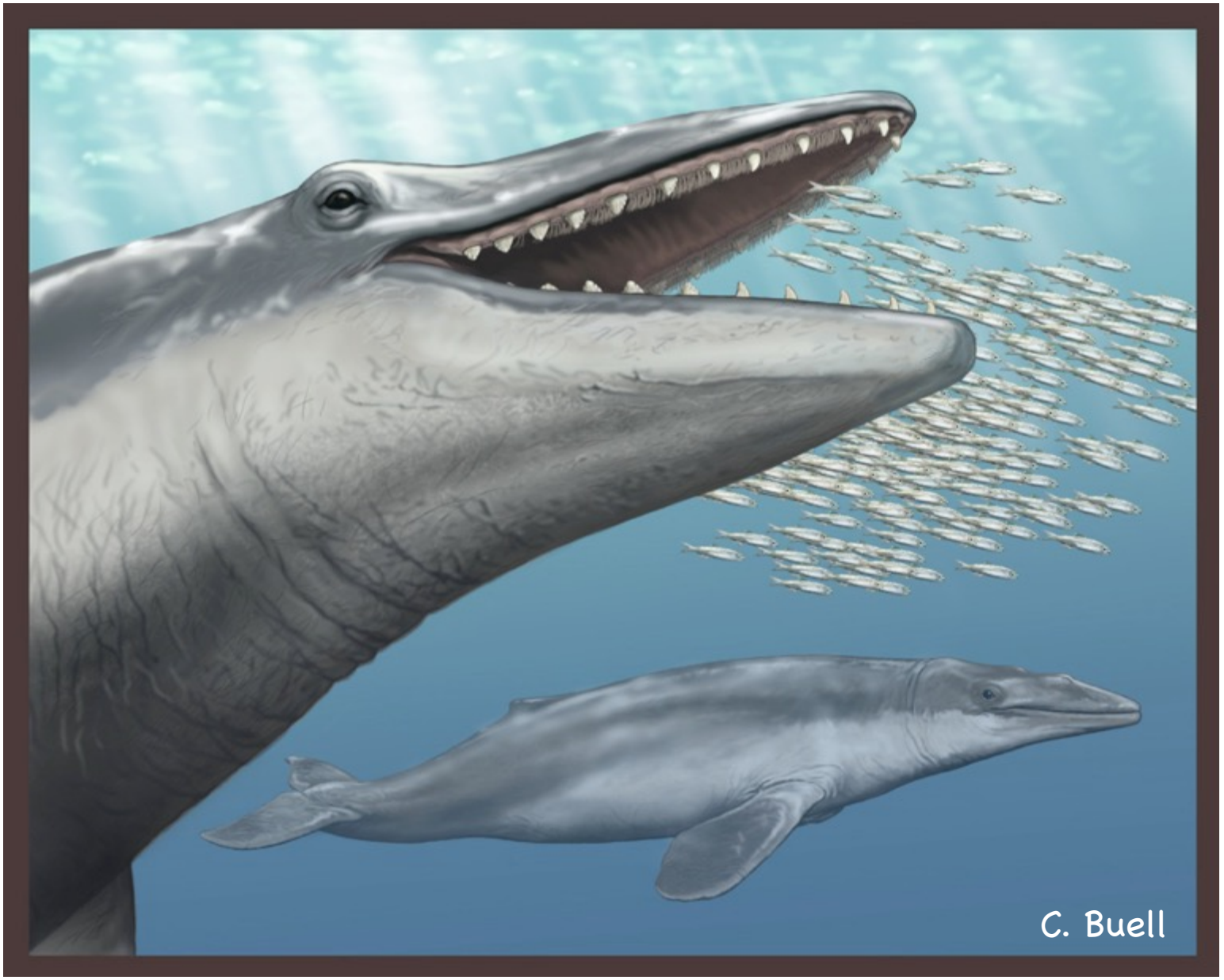
(modified Deméré and Berta, 2008: figs. 1 & 5)

(ventral view)

(NMST-32711)

(ventral view)

Homologous structures?


C. Buell

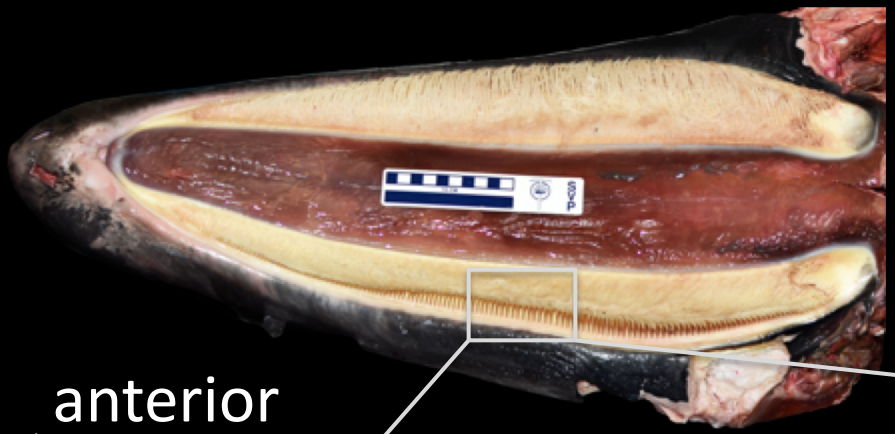
Gray whale neonate head Dissection

- live stranded January, 2012 Moss Landing, euthanized and head transported SDSU for dissection
- female calf 394 cm body length, weighing 225-320 kg., comparisons suggest <1 month old

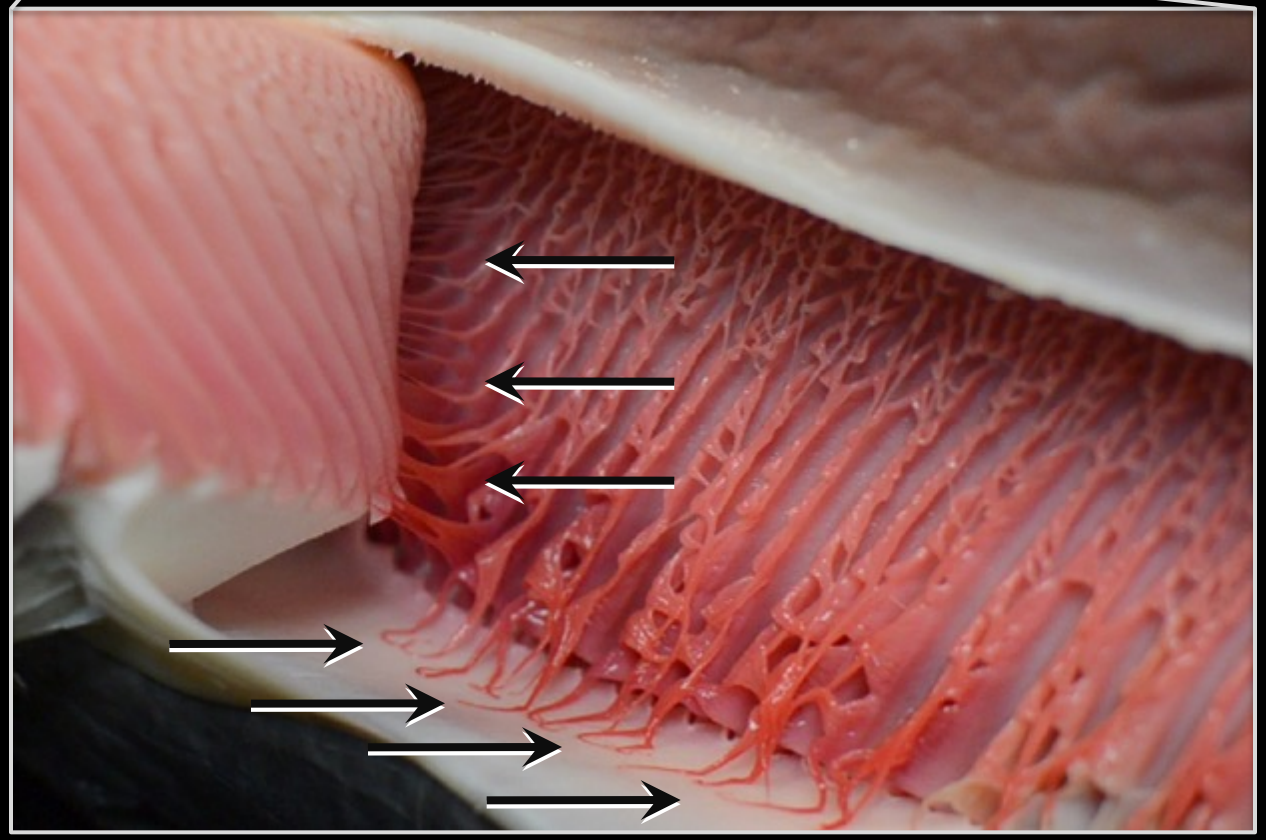
- neonate based on fetal folds and unhealed umbilicus

6 papers published
April, 2015
Anatomical Record

Dermal Papillae

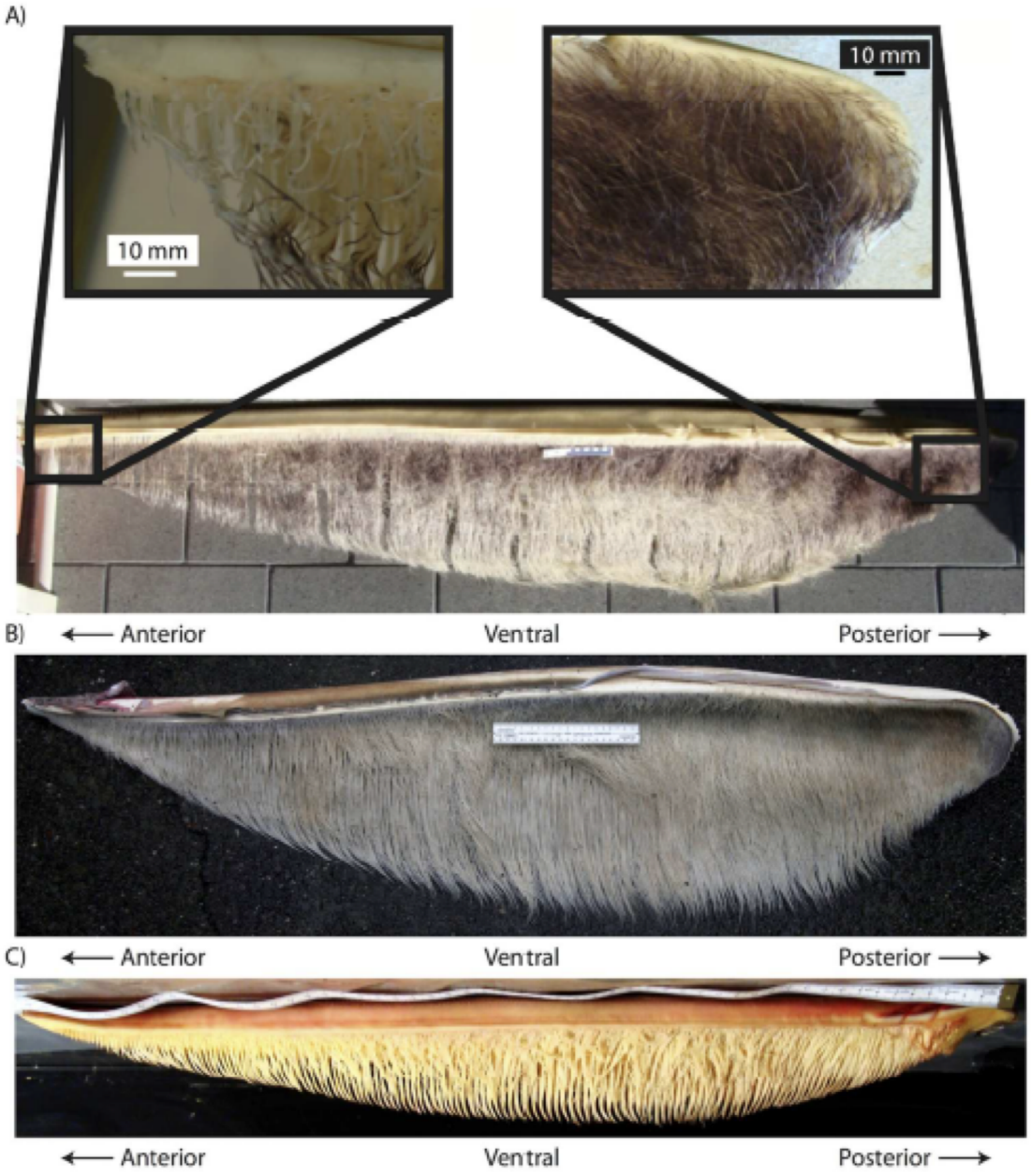


anterior



Gray whale neonate
(Eschrichtius robustus; SDNHM 25307)

Whole Gray Whale Baleen racks



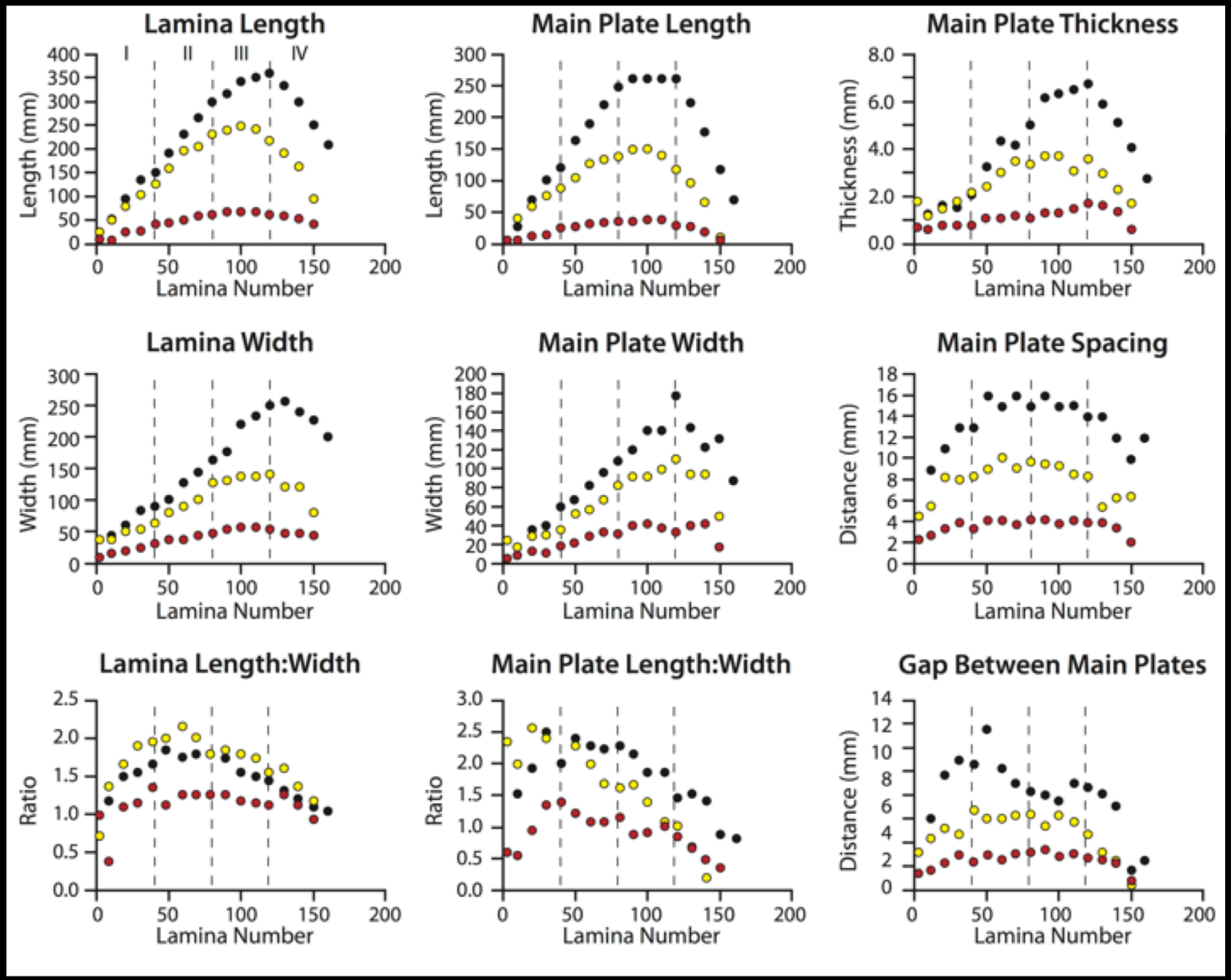
Adult (7–10 yrs)

Yearling

Neonate

Deméré, Ekdale, Berta and Zellmer 2015

Results Gray whale Baleen morphometrics



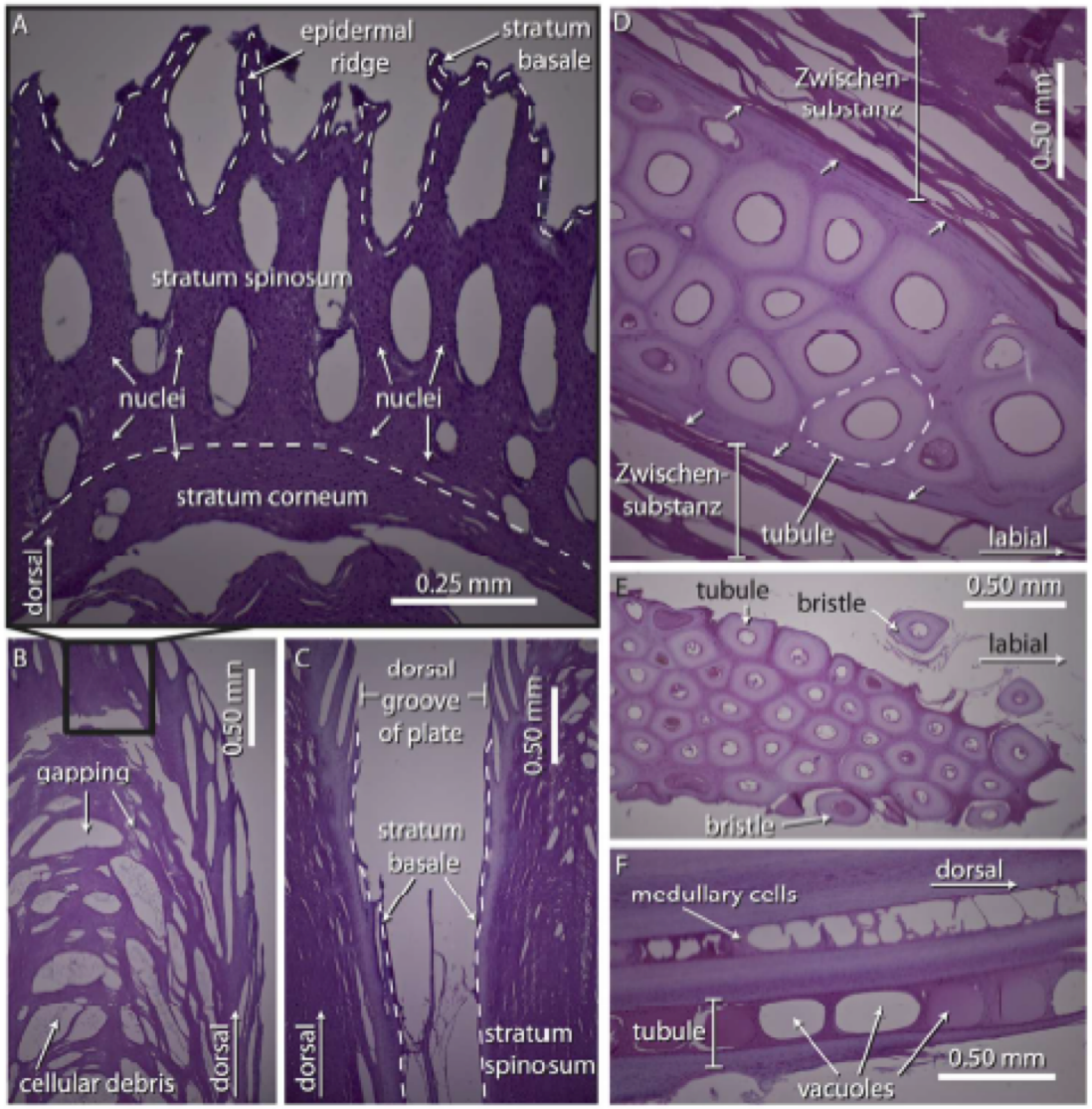
- Adult
- Yearling
- Neonate

Longest, widest, thickest plates posterior rack

= greatest filtration area

Young, Deméré, Ekdale, Berta and Zellmer 2015 *Anat. Rec*

Baleen



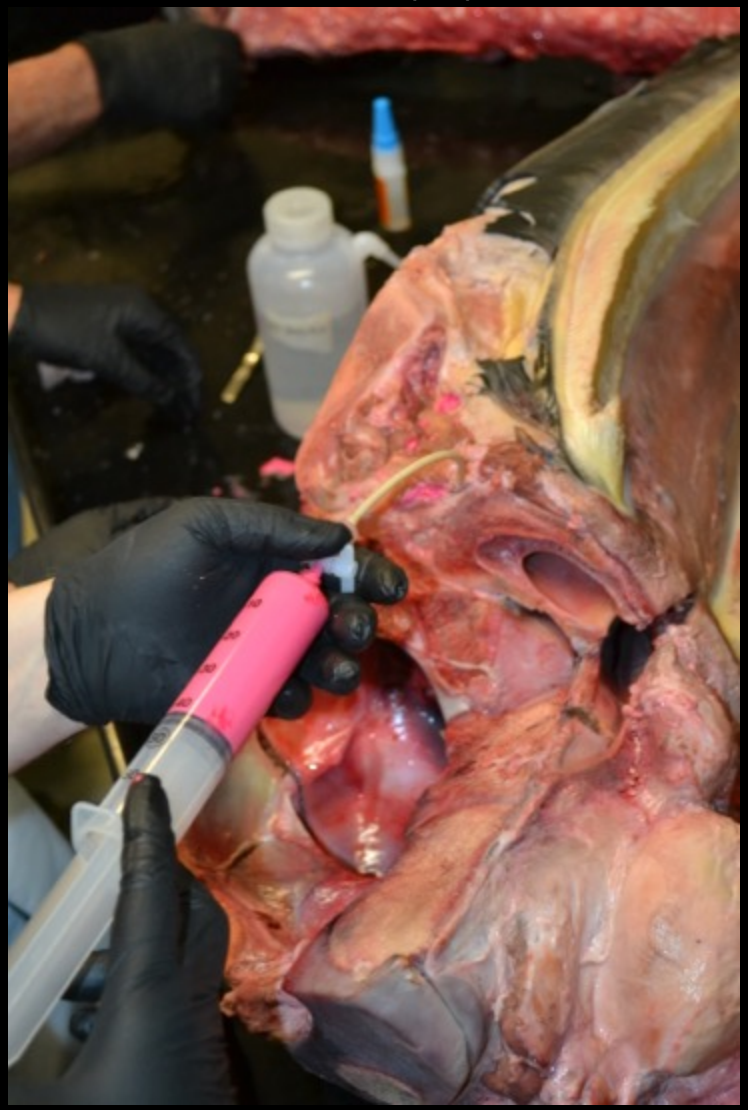
tissue
3 layers: basale, spinosum
corneum

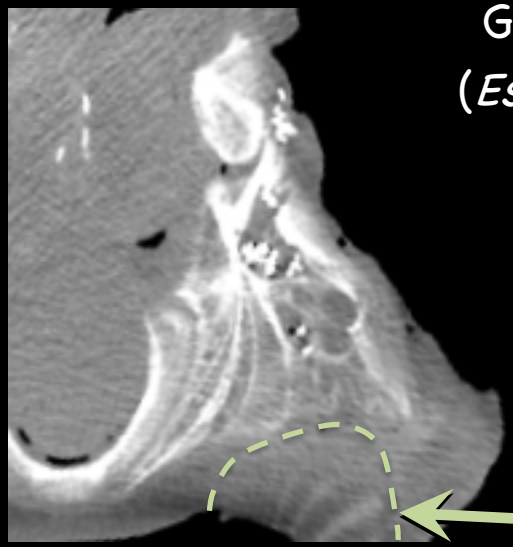
- baleen plates - invaginations of dermal tissue into Z substance

- baleen plate - tubules

Young, Deméré, Ekdale, Berta and Zellmer 2015 *Anat. Rec.*

Blood supply to Baleen-Modern whale

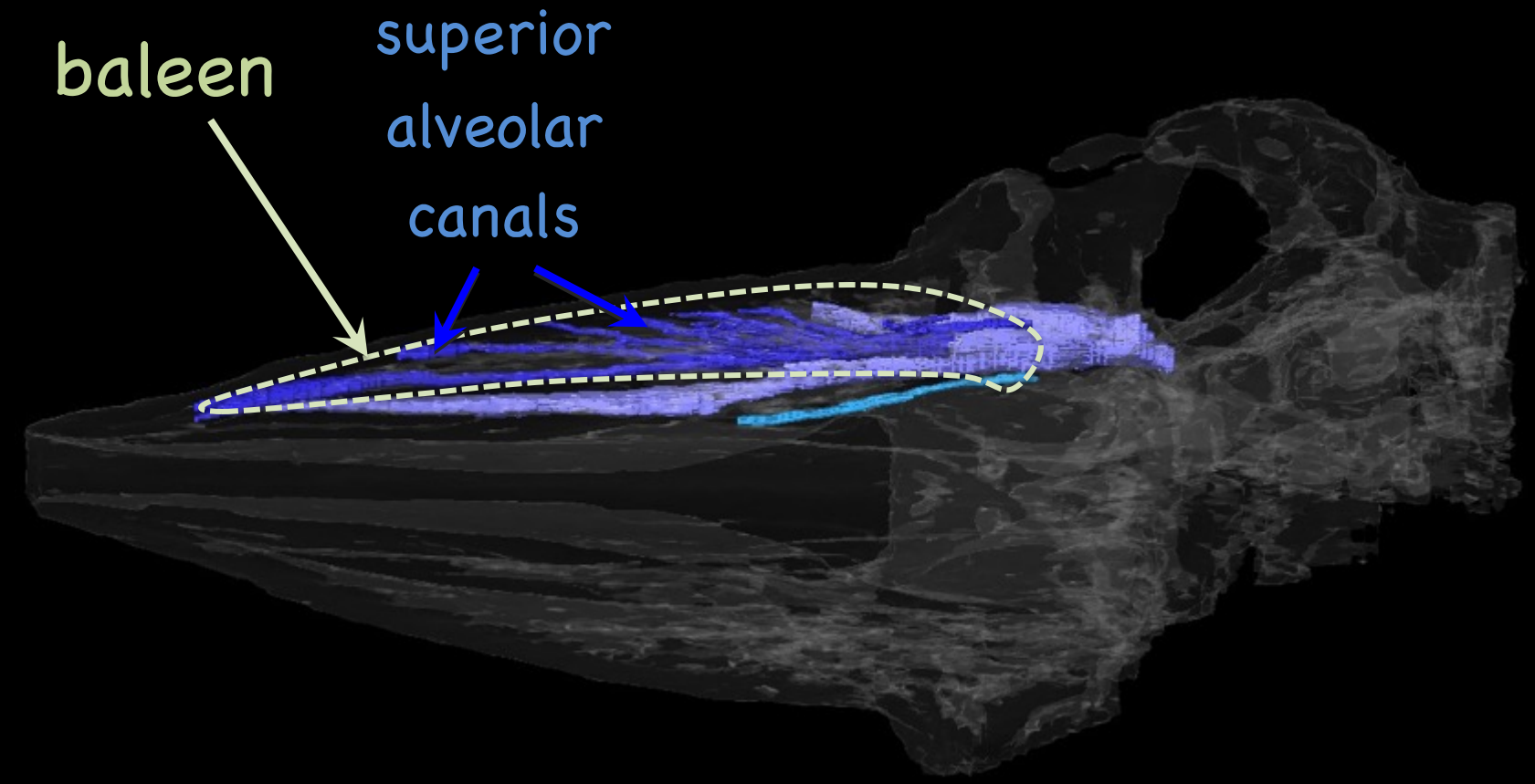




Gray whale neonate
(*Eschrichtius robustus*
SDNHM 25307)

dorsal

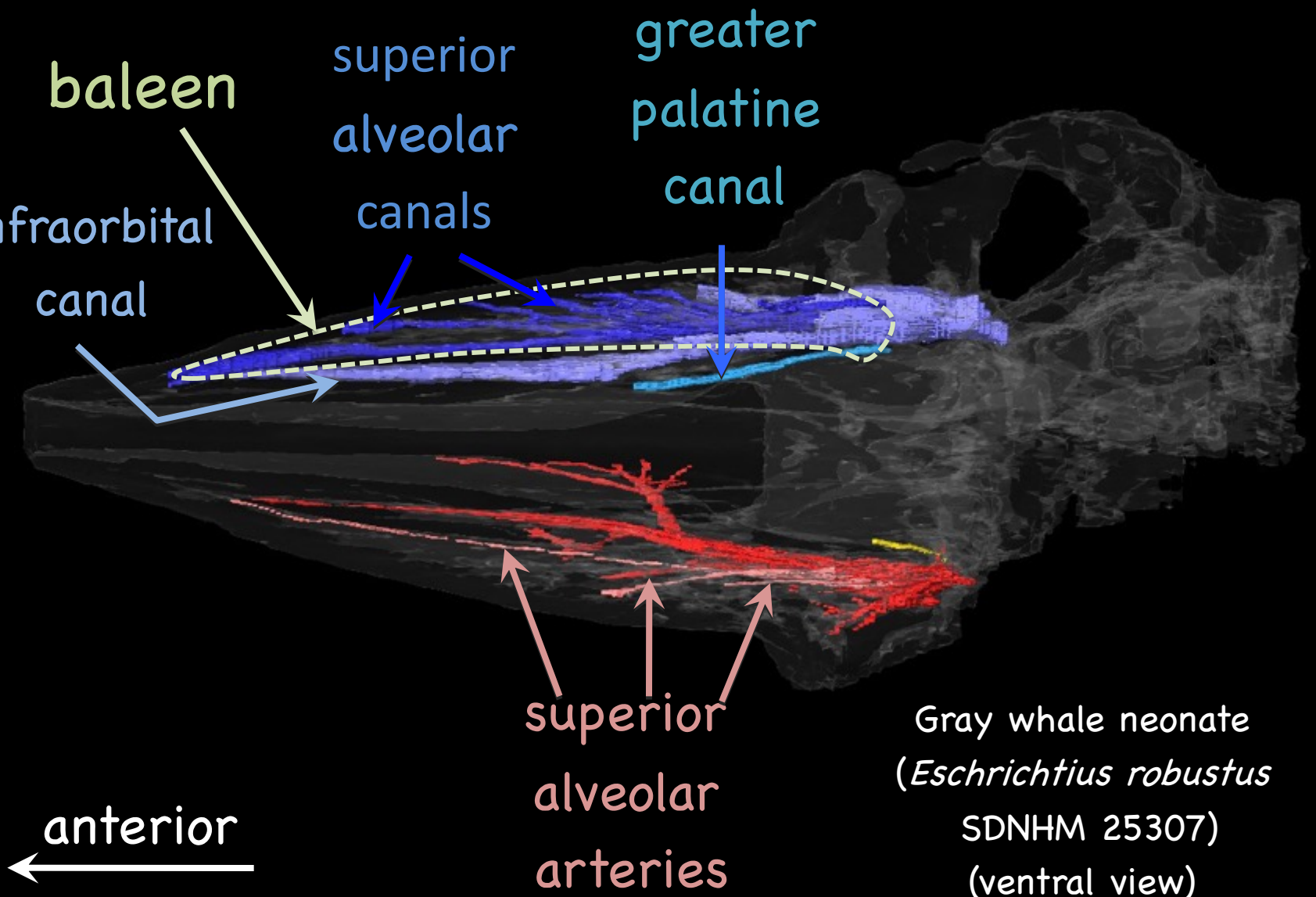
Bony Canals



anterior

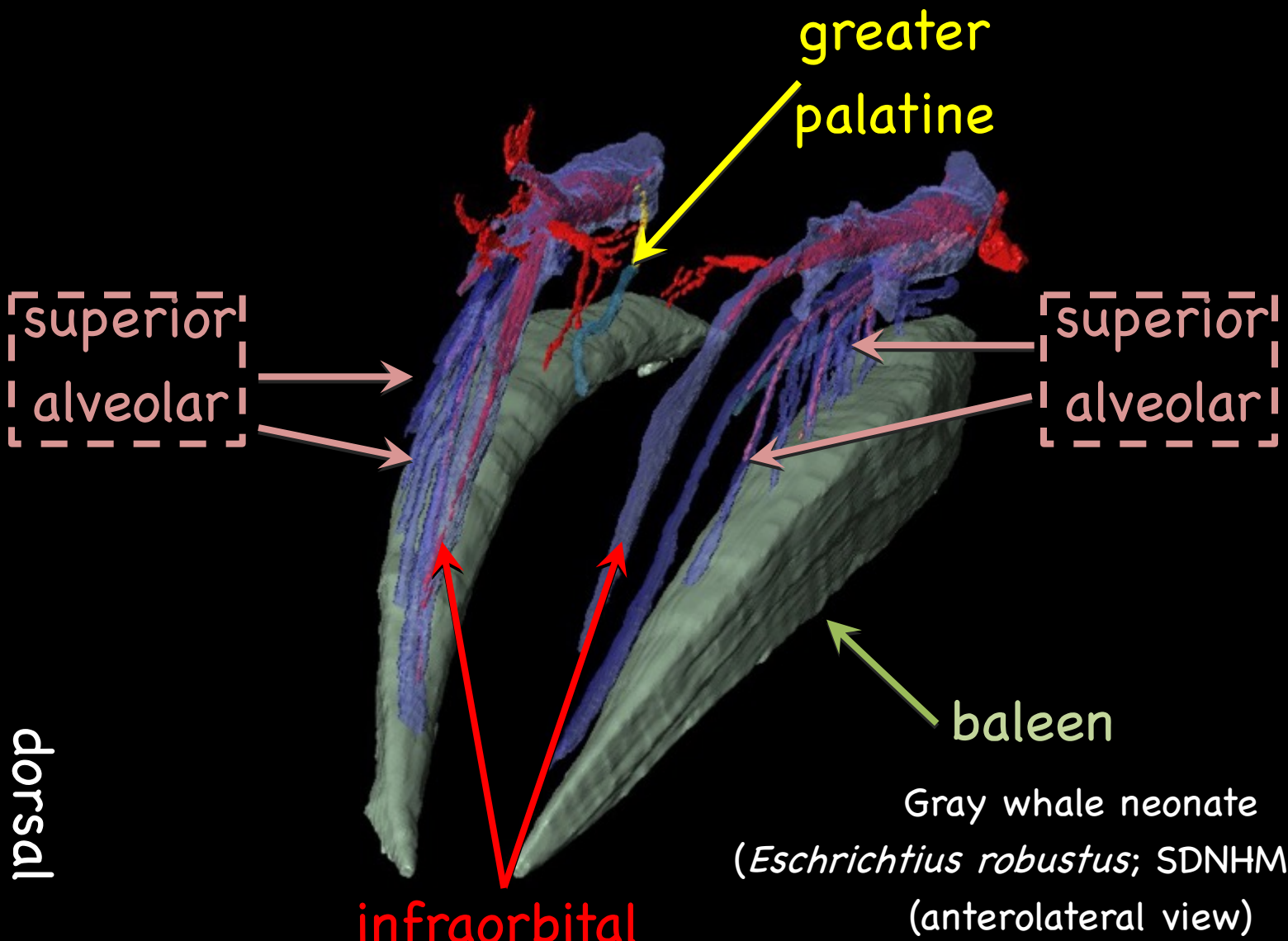
Gray whale neonate
(*Eschrichtius robustus*
SDNHM 25307)
(ventral view)
Ekdale, Deméré and Berta 2015

Arteries



Gray whale neonate
(*Eschrichtius robustus*
SDNHM 25307)
(ventral view)
Ekdale, Deméré and Berta 2015

Blood Source Confirmed

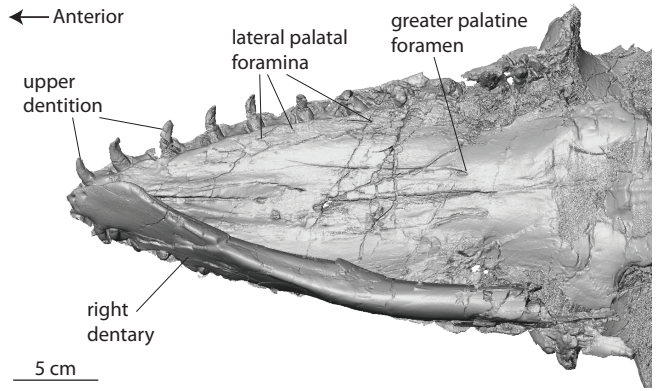


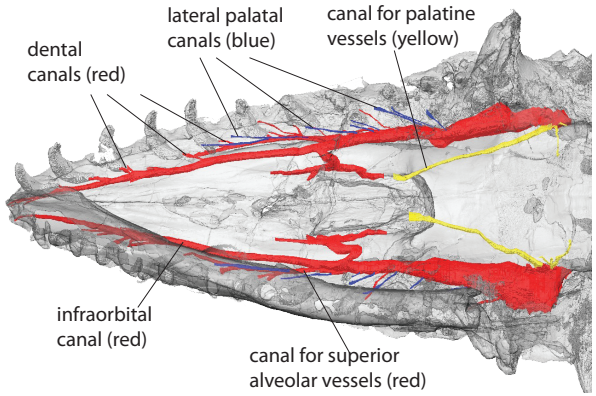
Gray whale neonate
(*Eschrichtius robustus*; SDNHM 25307)
(anterolateral view)

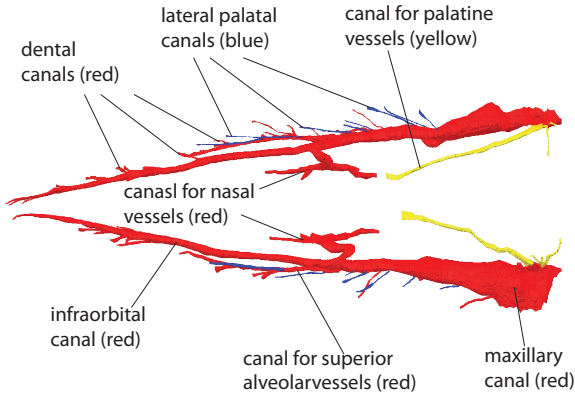
Ekdale, Deméré and Berta 2015

Update: CT scan of fossil mysticete

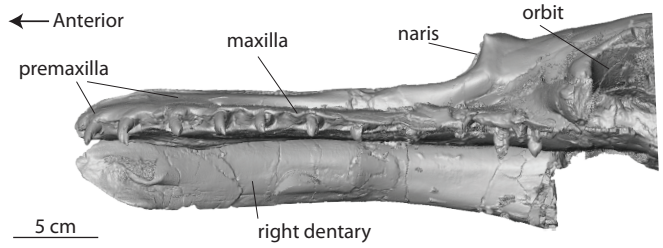
Aetiocetus weltoni (ventral view)

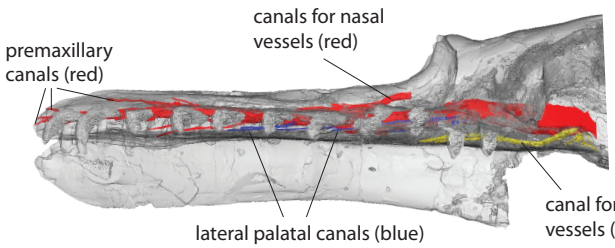


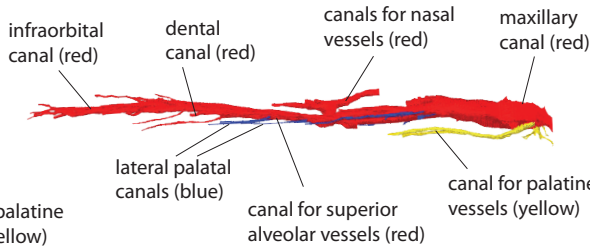




Aetiocetus weltoni (lateral view)



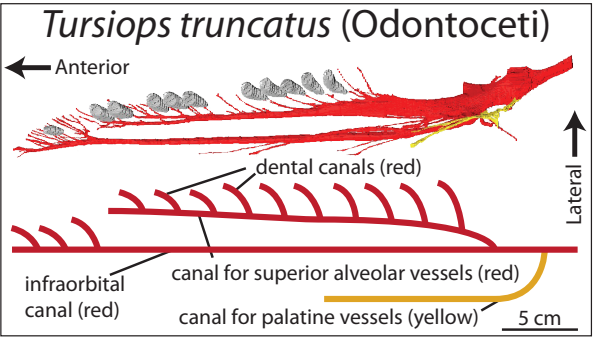


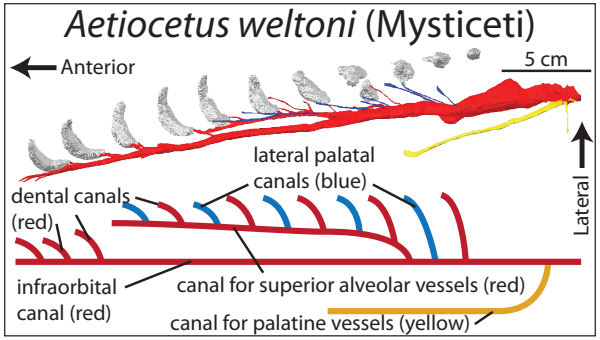


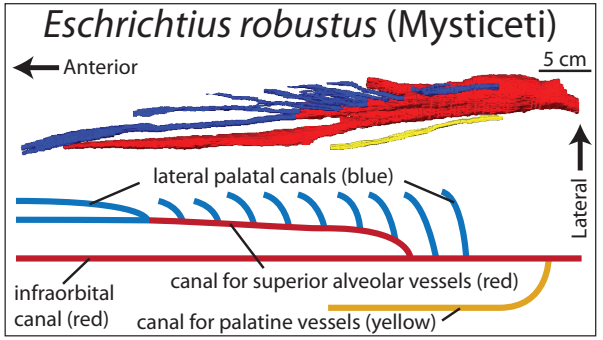
- homology of foramina and sulci in fossils questioned
- morphology (CT scans): 3 branches of artery-medial (yellow) palatine vessel, intermediate (red) premaxilla teeth and molars, lateral (blue)-palatal foramina

Ekdale and Deméré, in prep.

Comparative anatomy living and fossil whales







- branching pattern of vessels in fossil similar to living Odontocete (dolphin) and Mysticete (gray whale)
- lateral branch transmits sup. alveolar artery->teeth in dolphin (red) and lateral palatine foramina-> baleen (blue) in gray whale
- branching pattern supports teeth + baleen in fossil (red + blue)

Ekdale and Deméré, in prep.

Tooth genes

Genes	Function
Enamelin (*ENAM*)	enamel formation
Ameloblastin (*AMBN*)	enamel formation
Dentin Matrix Phosphoprotein 1 (*DMP1*)	dentin / bone formation

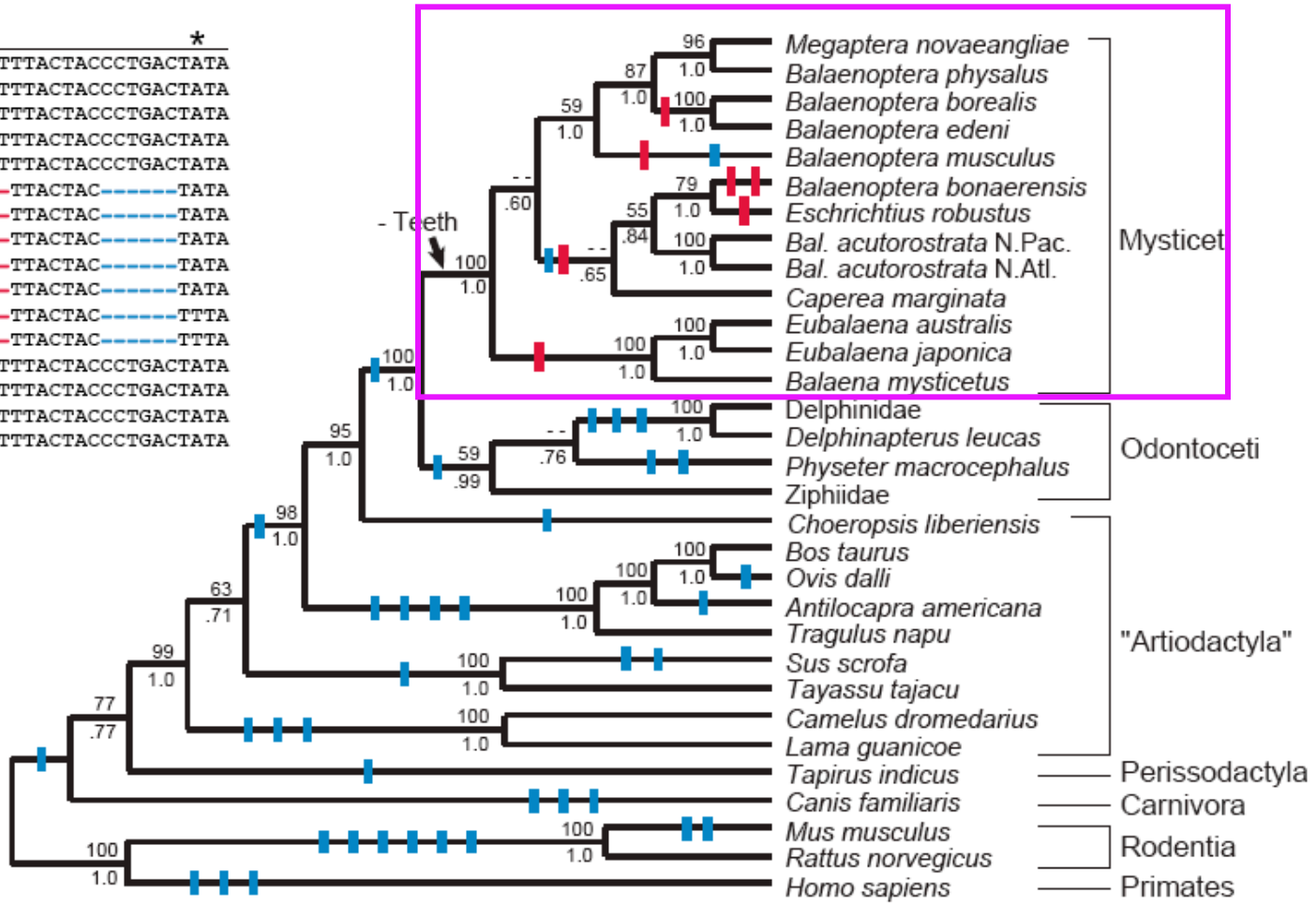
Amelogenesis Imperfecta

Prediction: Enamel-specific genes would be present in the baleen whale genome but would be non-functional.

Molecular changes in tooth genes

ENAM	*	*
M.nov.	GATGTGTTTACTACCCTGACTATA	
B.phy.	GATGTGTTTACTACCCTGACTATA	
B.mus.	GATGTGTTTACTACCCTGACTATA	
B.bor.	GATGTGTTTACTACCCTGACTATA	
B.ede.	GATGTGTTTACTACCCTGACTATA	
B.bon.	GACGTG-TTACTAC------TATA	
B.acu.1	GACGTG-TTACTAC------TATA	
B.acu.2	GACGTG-TTACTAC------TATA	
E.rob.1	GACGCG-TTACTAC------TATA	
E.rob.2	GACGCG-TTACTAC------TATA	
C.mar.1	GACGTG-TTACTAC------TTTA	
C.mar.2	GACGTG-TTACTAC------TTTA	
B.mys.	GACGTGTTTACTACCCTGACTATA	
E.aus.	GACGTGTTTACTACCCTGACTATA	
E.jap.	GACGTGTTTACTACCCTGACTATA	
P.mac.	GACGTGTTTACTACCCTGACTATA	

a)



frameshift mutation

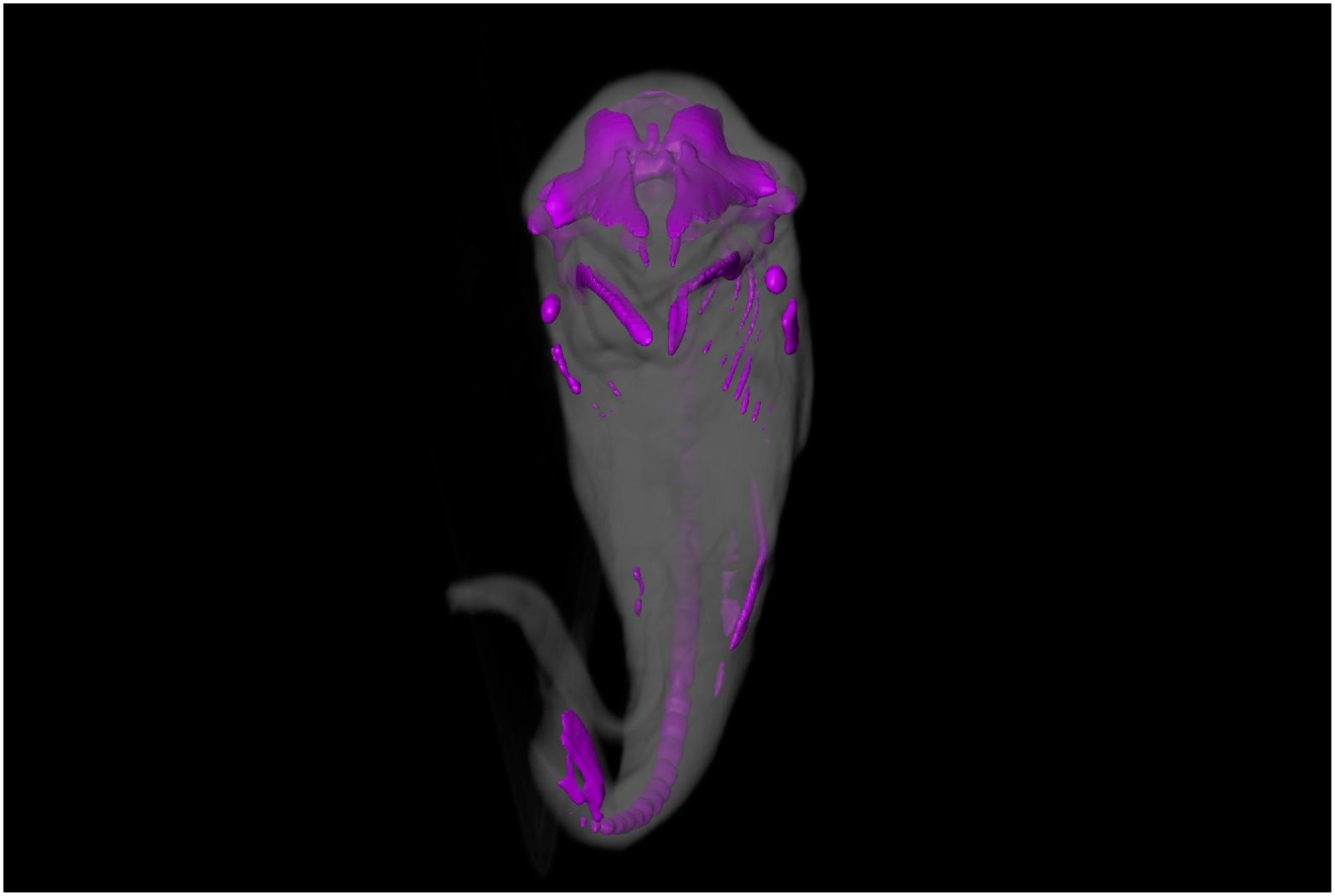
indel in multiple of 3 bases

Deméré, McGowen, Berta, and Gatesy, 2008 *Syst. Biol.*

Development: Teeth to Baleen Transition

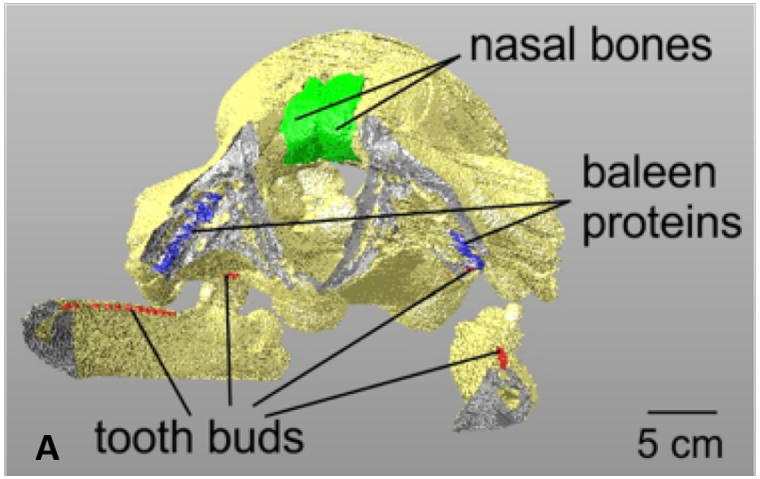
SDSU/UCR Evol. Biol. Ph.D. student: Agnese Lanzetti

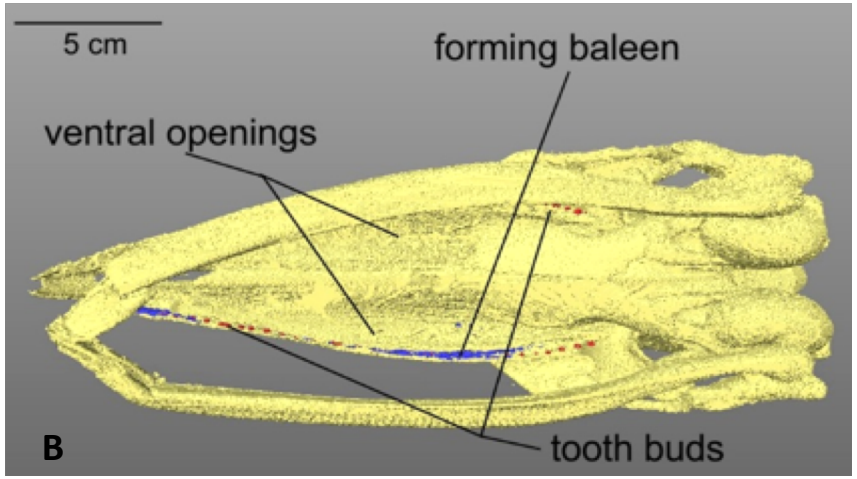
Humpback fetus 70+ days



Hypothesis: Co-occurrence of Teeth and baleen

- Embryological evidence: Tooth germs/buds + baleen proteins
- Requires additional testing (e.g. histology) for confirmation
- Baleen development posterior to anterior

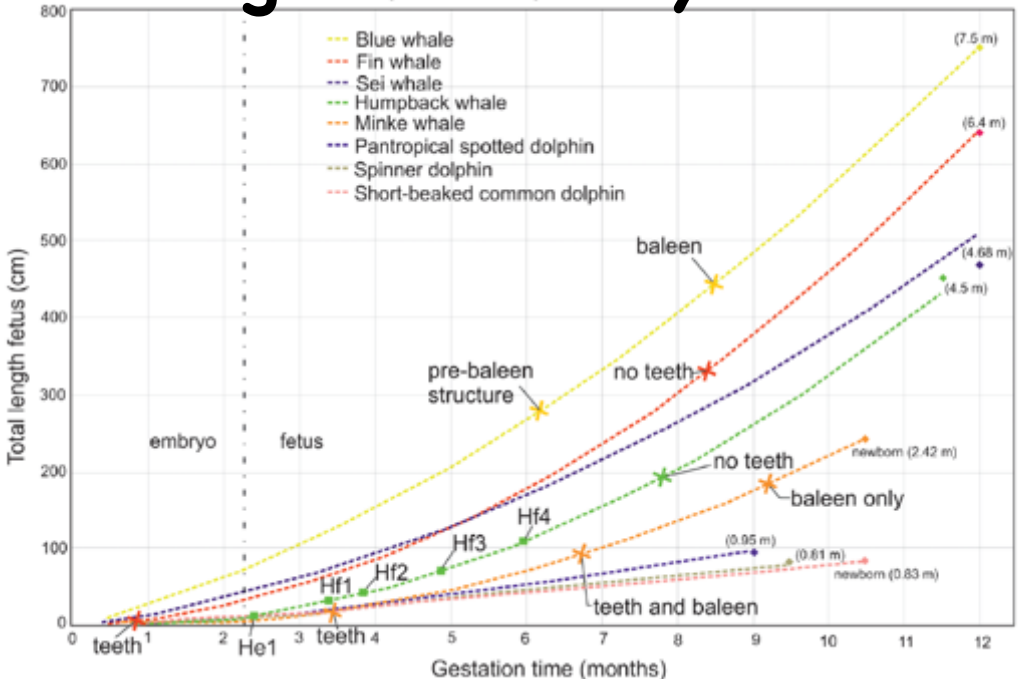


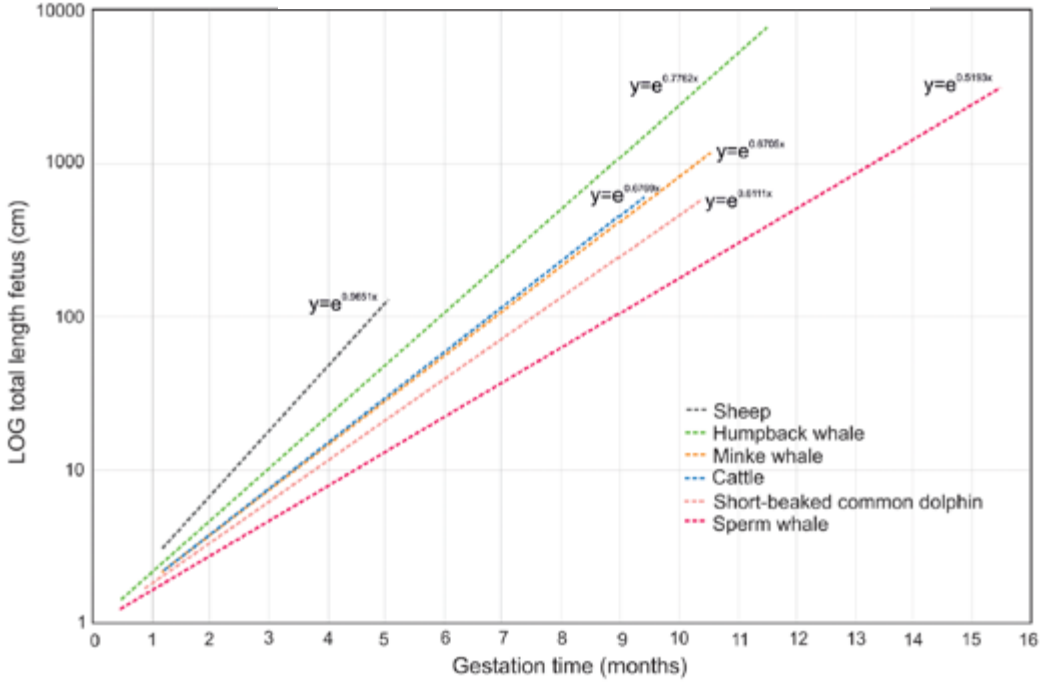


Minke whale fetus 7-8 months old – A: cross section; B: ventral view

Lanzetti, Berta, Ekdale 2018

Fetal growth in mysticetes and odontocetes





- Accelerated growth in mysticetes vs odontocetes
- Teeth and baleen co-occur
- Teeth-to-baleen transition in mysticetes: 7-9 months

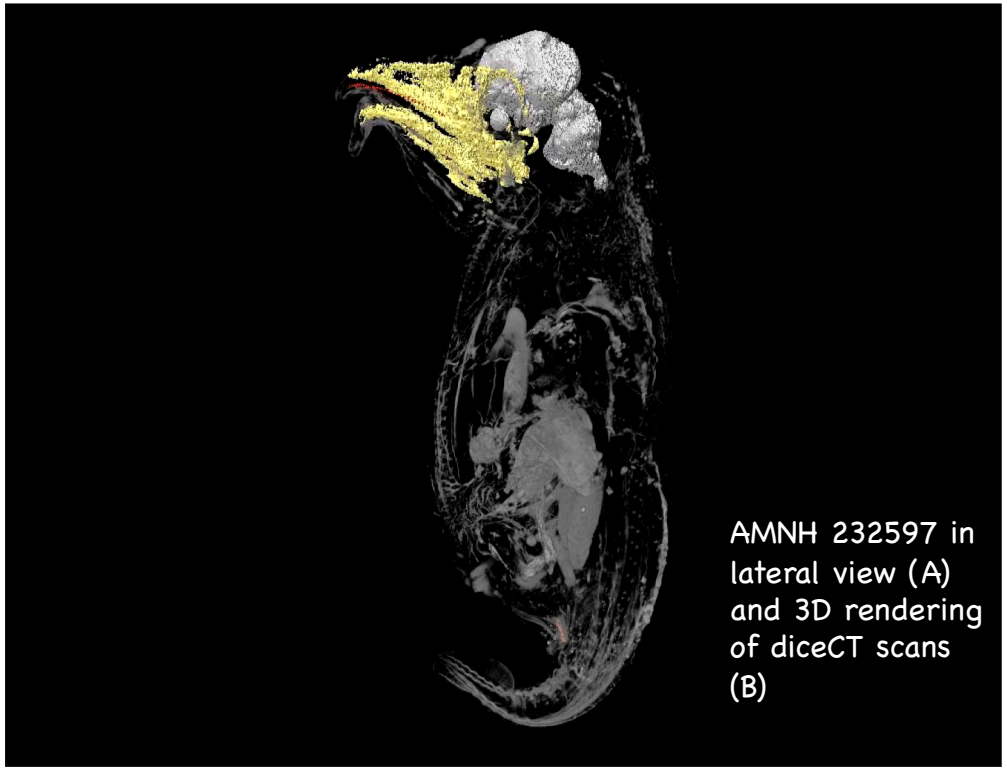
Lanzetti, Berta, Ekdale 2018

Specimen He1

- Carnegie stage 17/18

(ca. 2 months)

- Initiation of ossification in rostrum and mandible
- No endochondral ossification
- Tooth germs (red) present
  - upper jaw 20+ each side
  - lower jaws more sparse, less than 10 each side
- Only postcranial ossification- pelvic elements



AMNH 232597 in lateral view (A) and 3D rendering of diceCT scans (B)

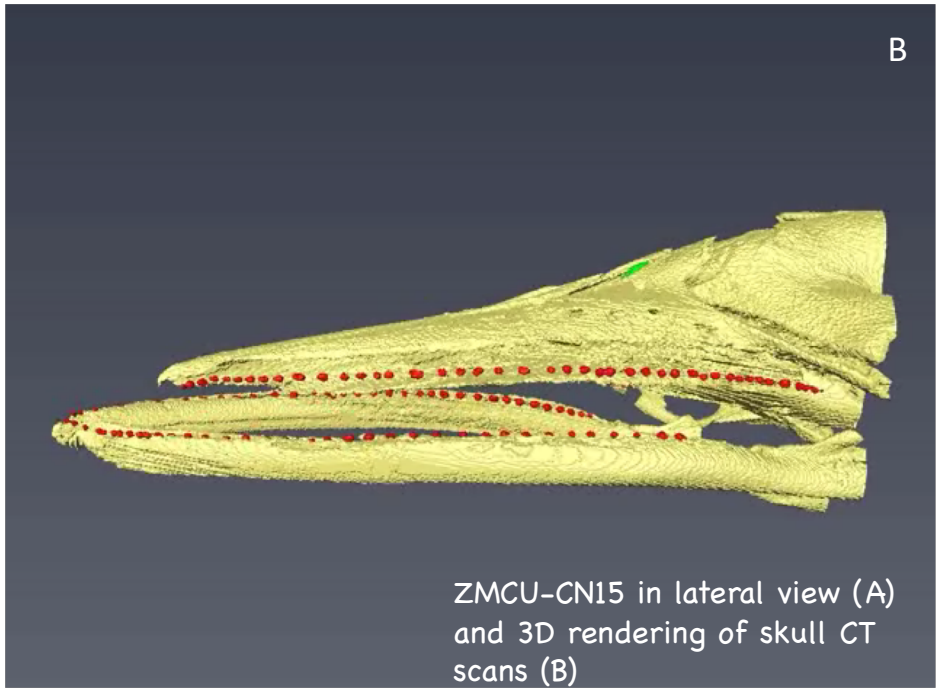
Lanzetti, Berta, Ekdale 2018

Specimen Hf4

- Fetal stage 24

(ca. 6 months)

- Ossification mostly complete
- More foramina in palatine and maxilla
- Tooth germs:
  - 40 each upper jaw, alveolar groove smaller
  - 36-38 each lower jaw, groove shallower



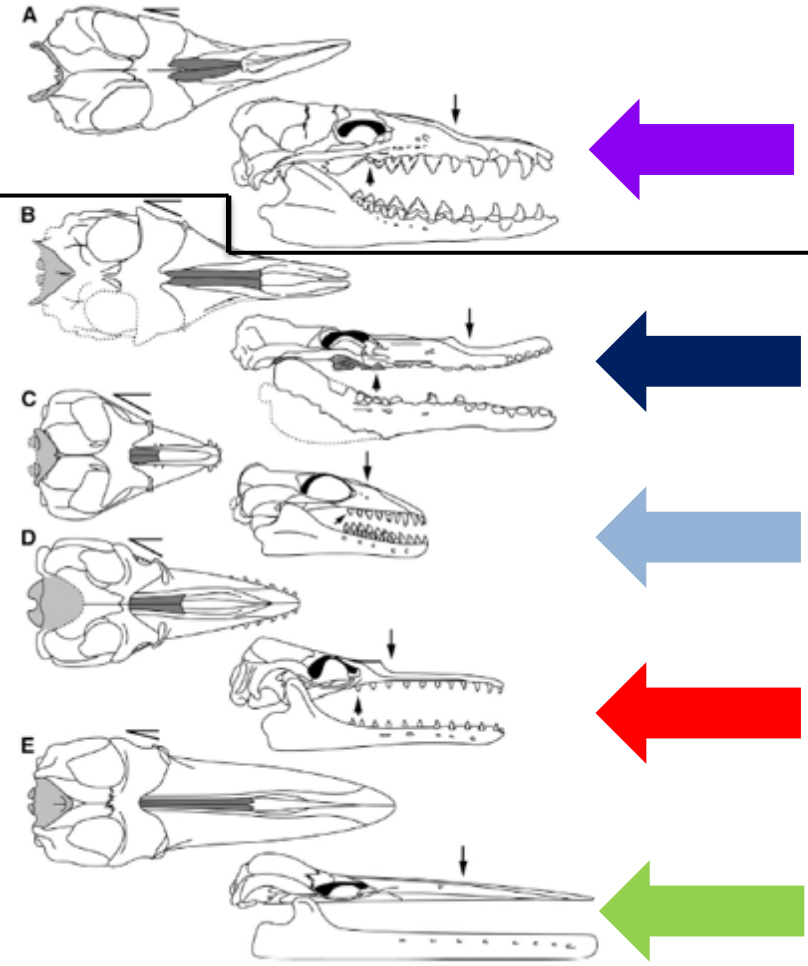
ZMCU-CN15 in lateral view (A) and 3D rendering of skull CT scans (B)

Lanzetti, Berta, Ekdale, 2018

What we know…

1. What was the ancestral feeding strategy in baleen whales?

Earliest mysticetes evolved 36 Ma likely employed suction feeding but others used teeth



Biting with teeth

Ancestral whales

Suction with/out teeth?

Baleen whales

Filter with teeth

Filter with teeth and baleen

Filter with baleen

What we know….

2. When and how did tooth loss occur and baleen evolve?

- anatomical and fossil evidence of tooth loss and replacement with baleen – 7-9 months of gestation, at least 30 Ma

- lateral sulci and foramina on palate= osteological correlates of baleen in fossil stem mysticetes

- blood supply to baleen confirmed-superior alveolar arteries

- presence of pseudogenes in mysticete genome confirm their toothed heritage

- teeth resorbed and lost followed by baleen development (anatomical, embryological and genetic evidence) from back to front of mouth

What we don't know...

- many new fossils but no comprehensive phylogeny of fossil and extant mysticetes
    earliest mysticetes exploring different feeding strategies- biting, filter and suction

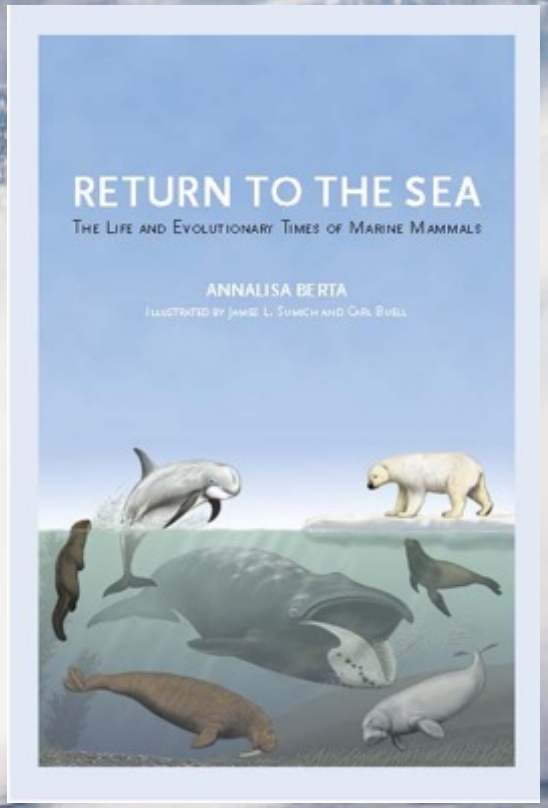
- lack of evidence/speculation about functional basis for teeth + baleen
    proto-baleen different than modern baleen

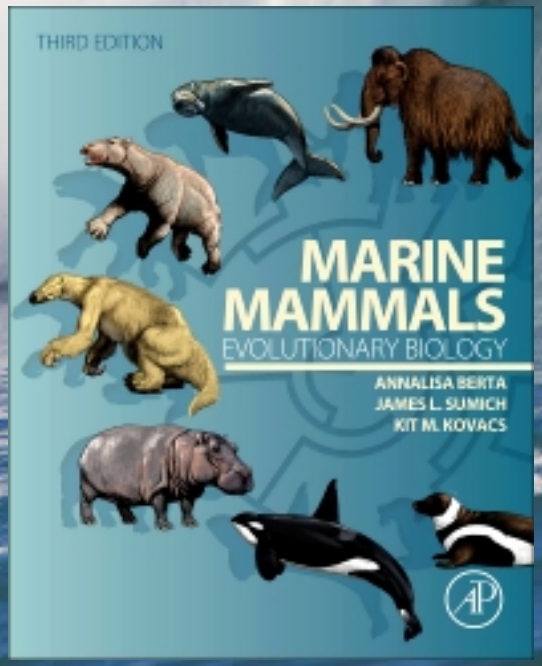
- blood supply to gum tissue not baleen
    CT scans upper jaw show gums + baleen

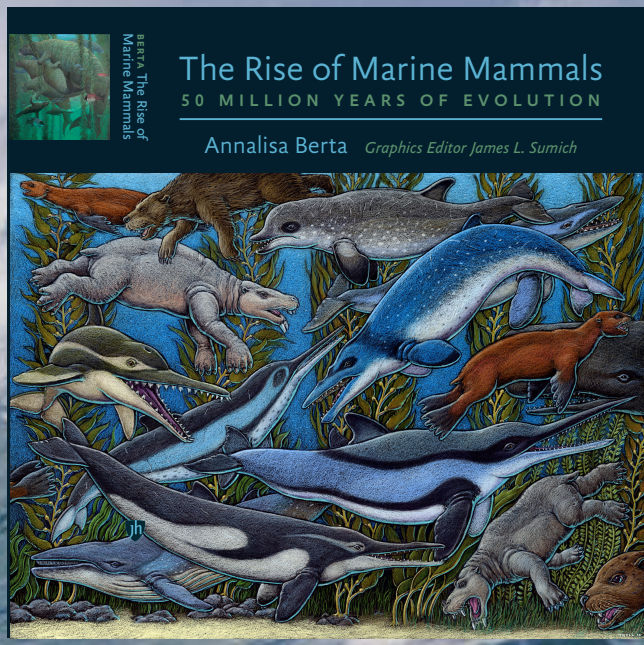
Moving forward…

- Biomechanical modeling studies of tooth wear and feeding in extinct mysticetes
- Histological study of "baleen" proteins
- Sequencing of baleen genes
- Gene expression patterns in keratinous feeding structures of close artiodactyl relatives (hippo, cow, sheep, deer)
- Need for **interdisciplinary efforts**

QUESTIONS?

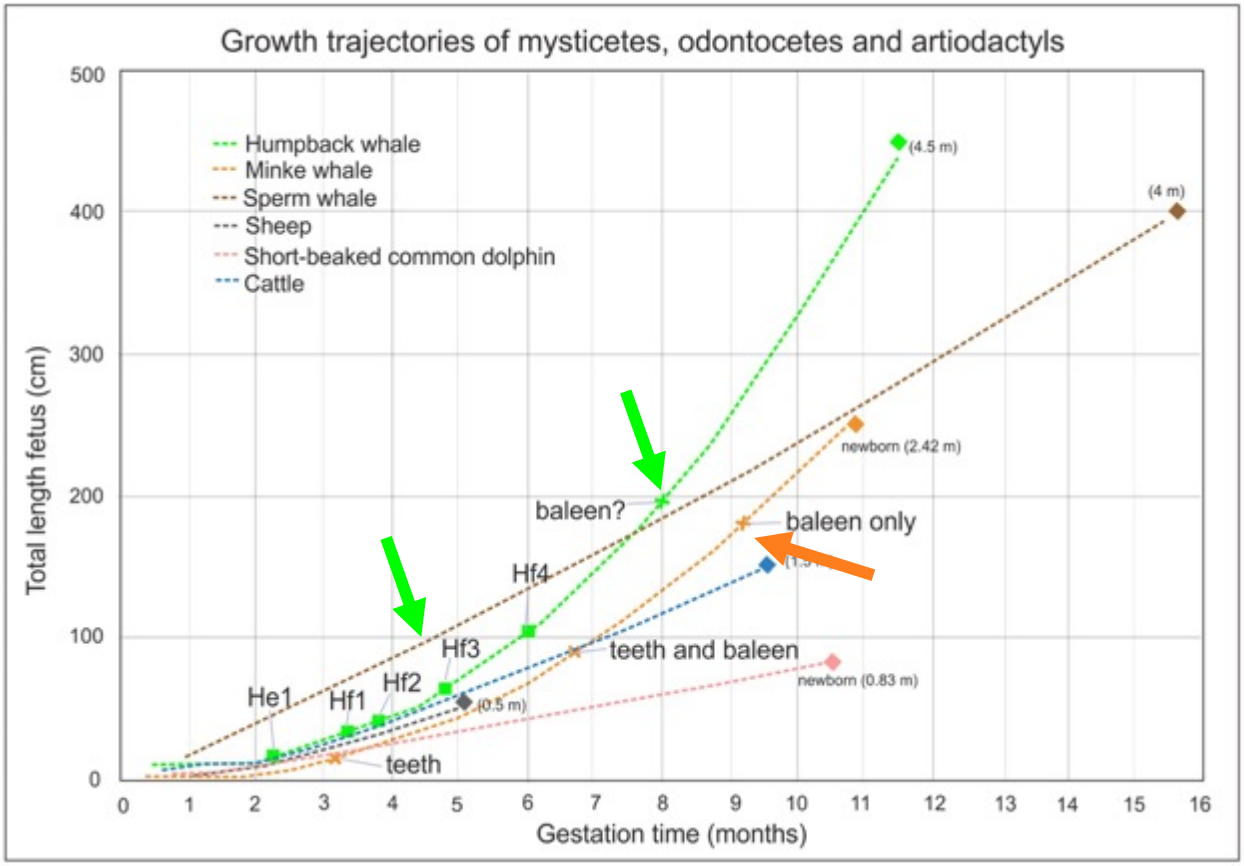




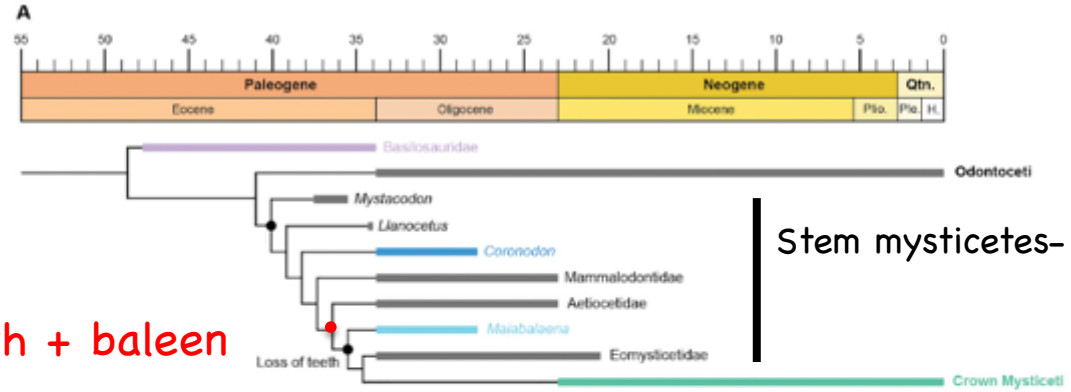


Self promotion...

Aging the specimens

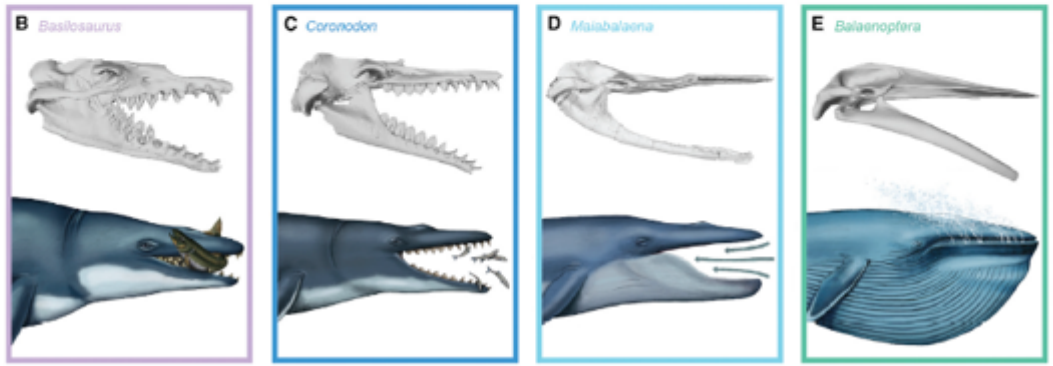


Mysticete Phylogeny, Feeding and Tooth-Baleen Transition



Stem mysticetes- biting, suction, filter

Teeth + baleen



Biting

Filter Feeder?

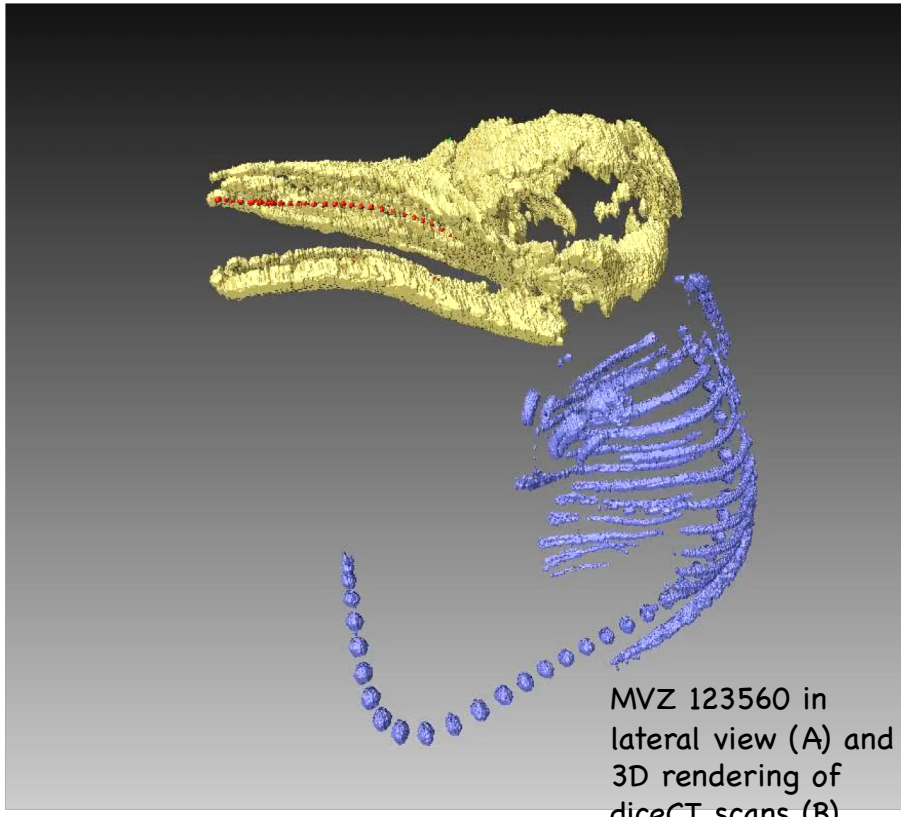
Suction Feeder?

Engulfment/Lunge feeding

Modified from Peredo et al. 2017

Specimen Hf2

- Fetal stage 20 (ca.4-5? months)
- Rostrum clearly defined, infraorbital foramina on maxilla
- Supraoccipital present and elongated anteriorly
- Tooth buds:
  - 28-26 each upper jaw
  - 11-16 each left jaw, smaller
- Vertebrae centers, ribs, fore-limb bones

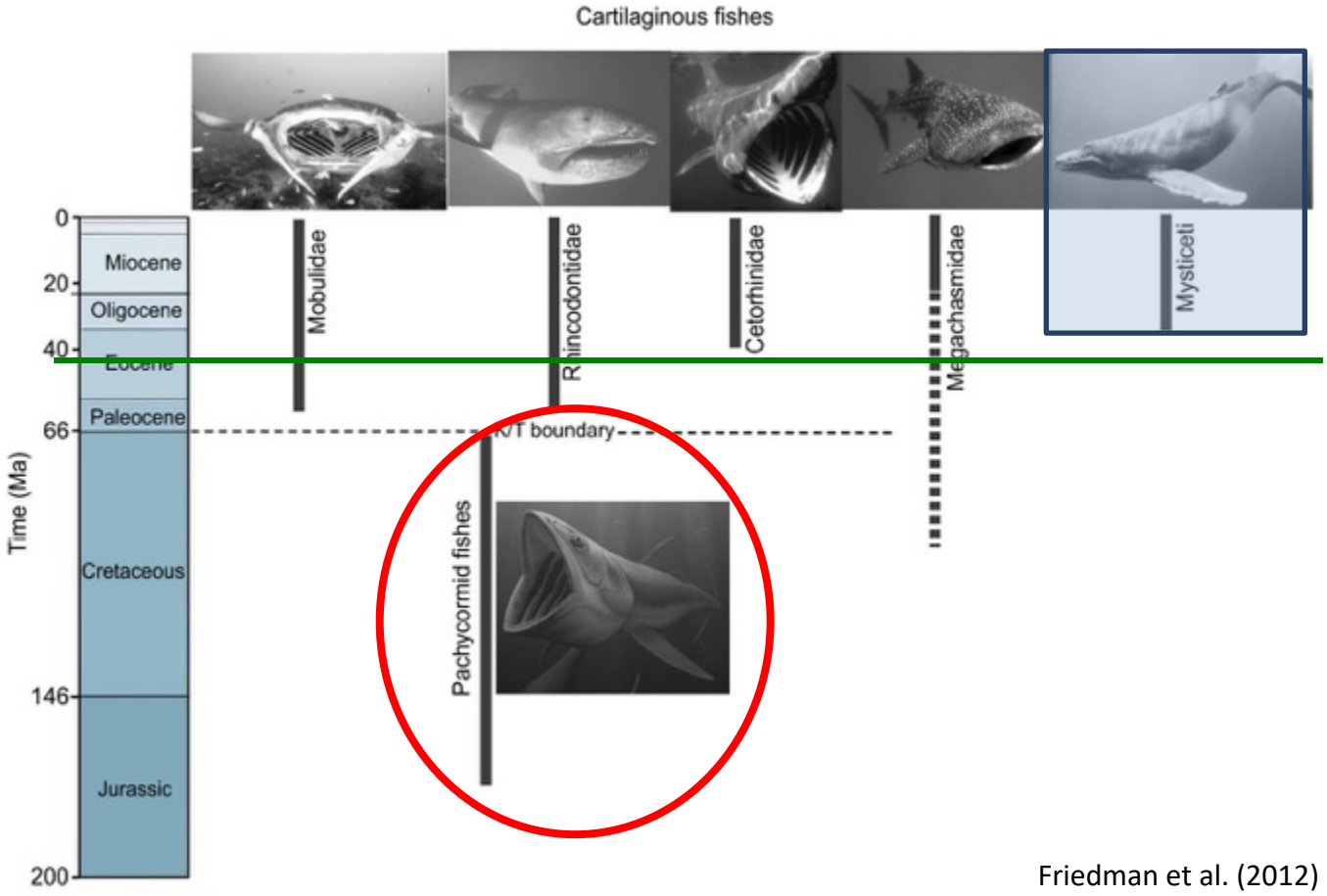


MVZ 123560 in lateral view (A) and 3D rendering of diceCT scans (B)

Future work

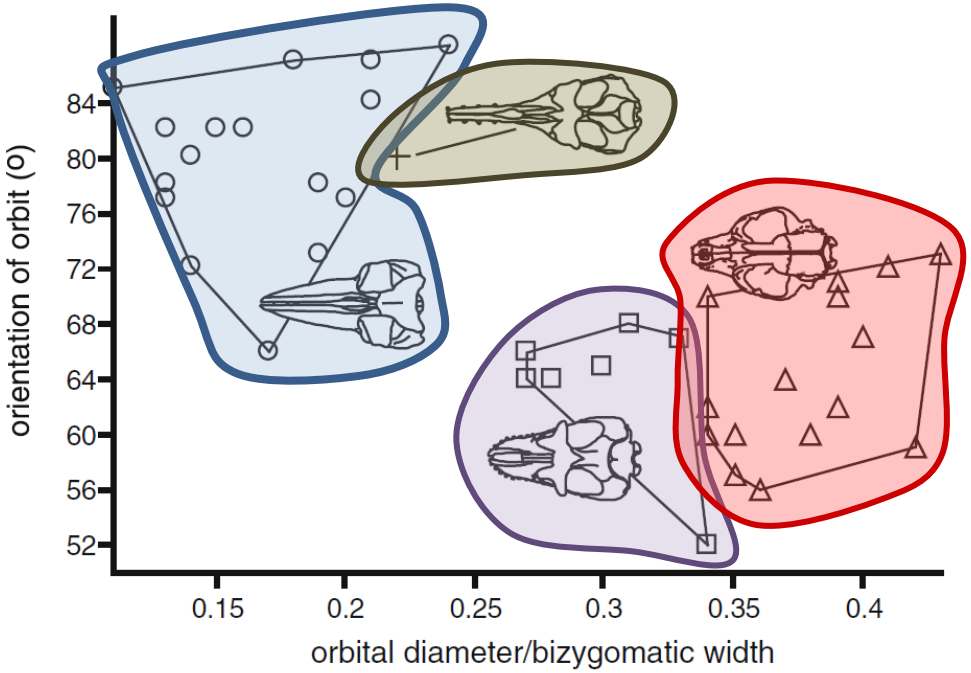
- New discoveries and re-description of fossil specimens
- More sequences of genes related to baleen whales feeding adaptations (e.g. teeth) should be collected, to trace the patterns and time of loss of function on the phylogeny
- Changes in ontogeny:
  - Shifts in timing of ossification among mysticetes and compared to other mammals – more characters to associate with bulk filter feeding
  - Shape of the skull and of the individual tooth buds – how they relate to ancestral condition

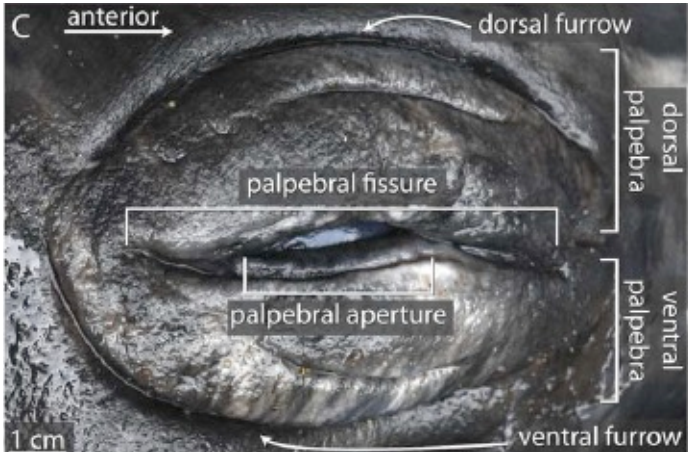
Filter feeding in fishes



Friedman et al. (2012)

Prey location: vision



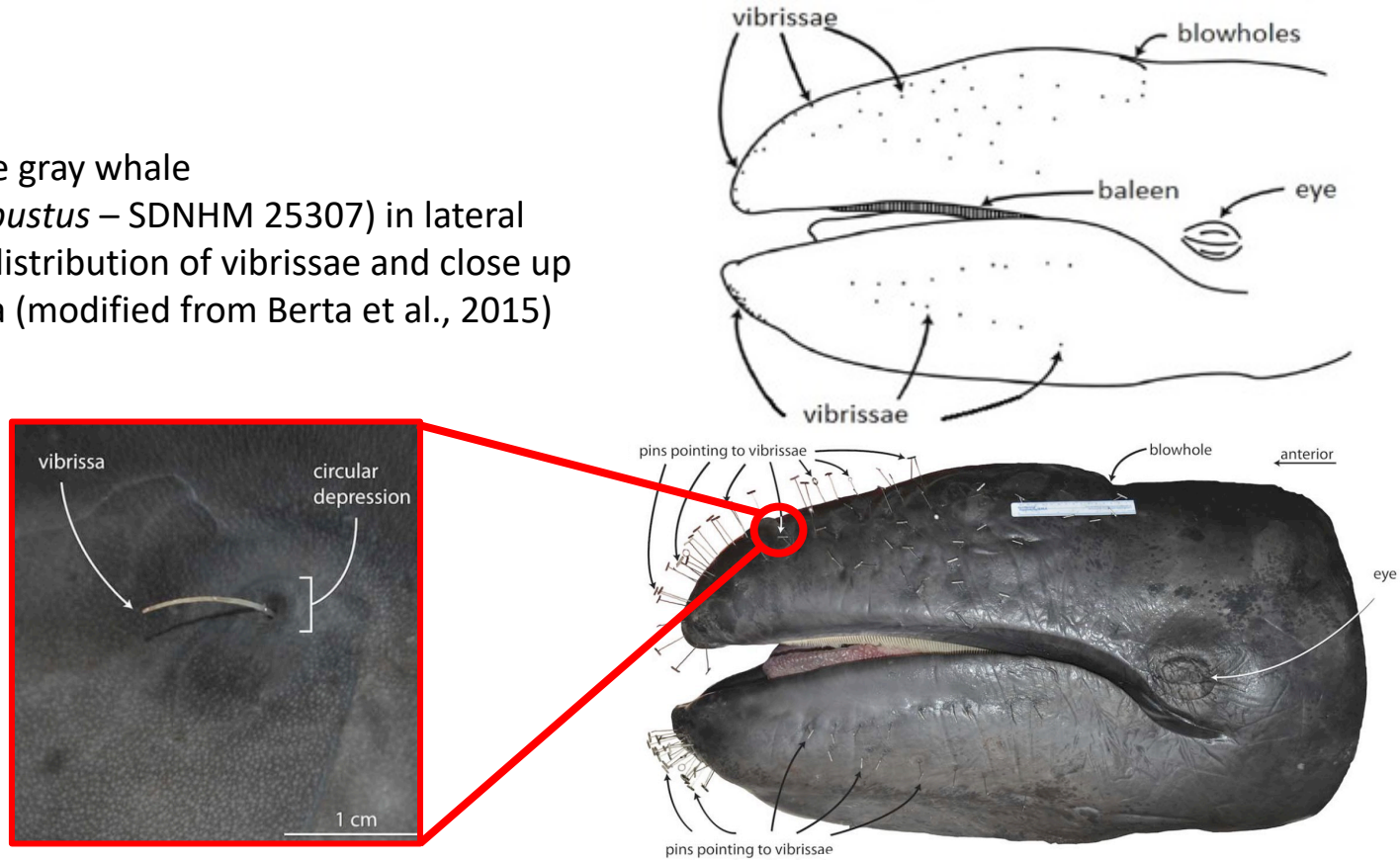


Left eye of a neonate gray whale (*Eschrichtius robustus* – SDNHM 25307) (modified from Berta et al., 2015)

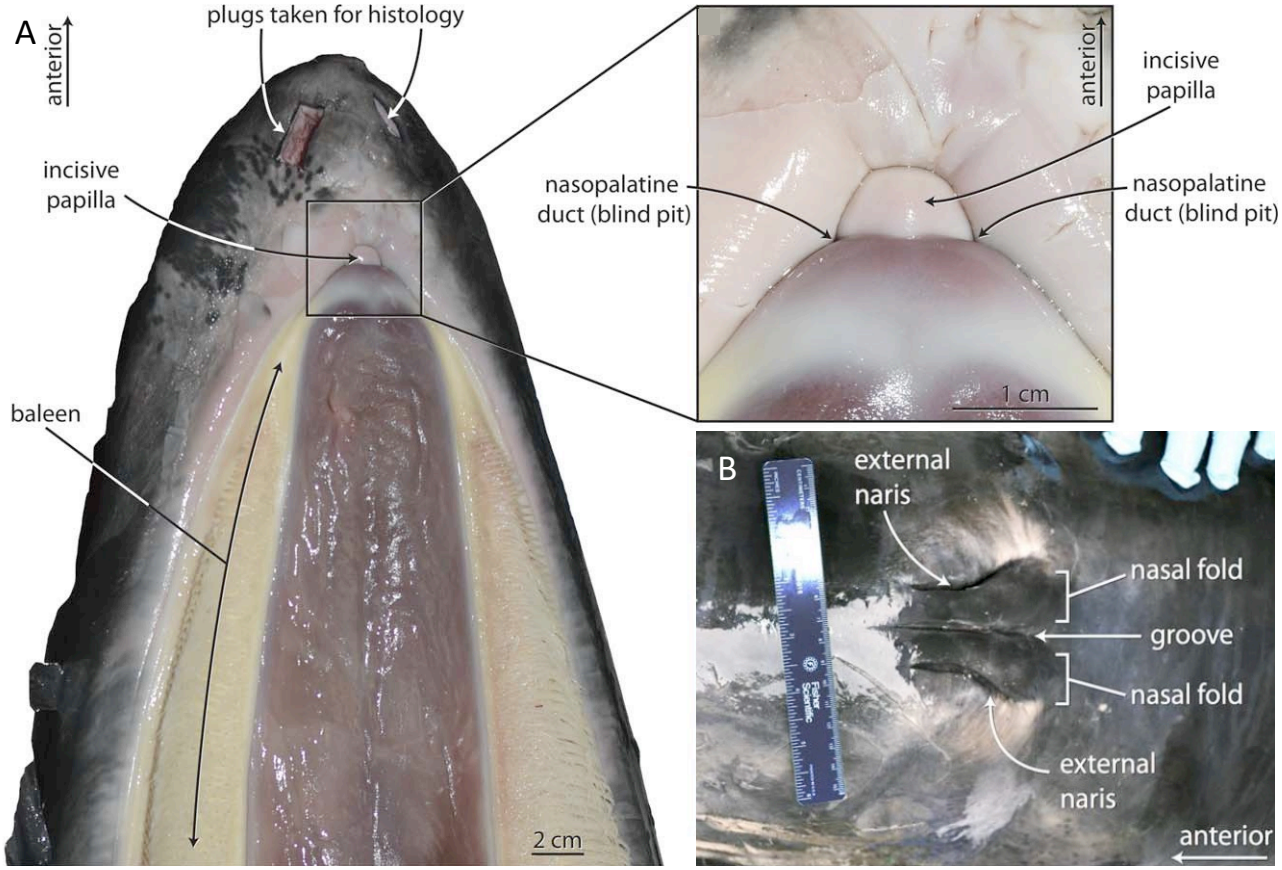
Plots of orbital diameter/byzigomatic width against orientation of the orbit (from Marx, 2011)

Prey location: vibrissae

Head of neonate gray whale (*Eschrichtius robustus* – SDNHM 25307) in lateral view, showing distribution of vibrissae and close up of single vibrissa (modified from Berta et al., 2015)

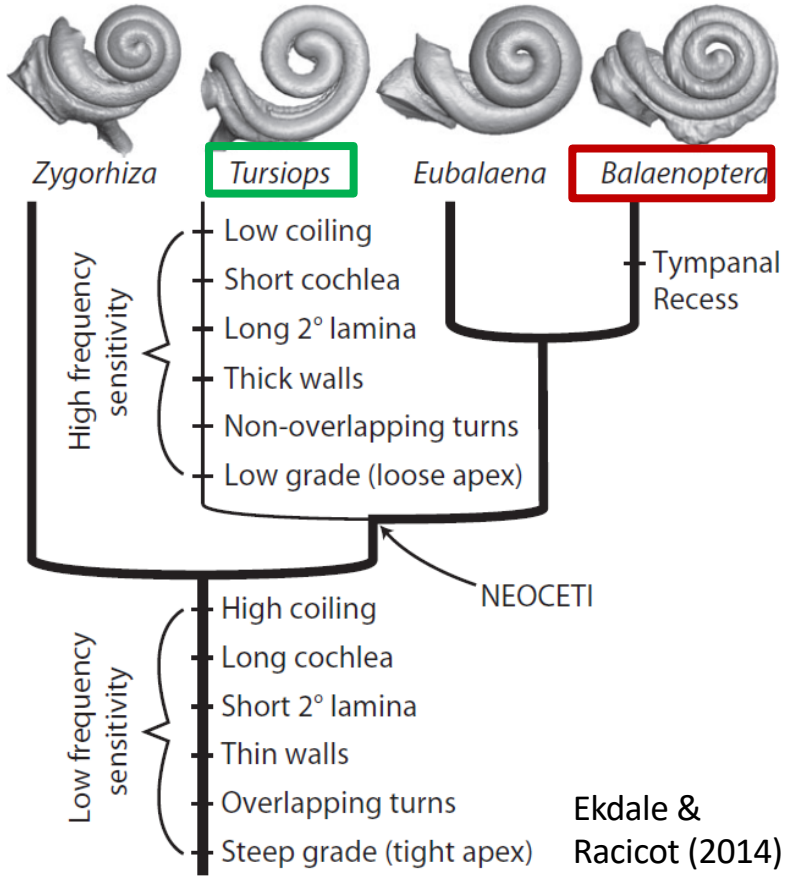


Prey location: olfaction

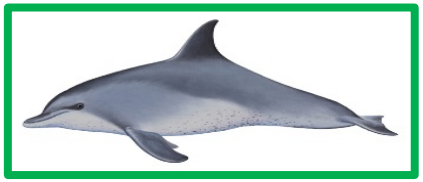


Neonate gray whale (*Eschrichtius robustus* – SDNHM 25307)
A) palate of in ventral view, with close up of incisive papilla and nasopalatine ducts
B) external nares
(modified from Berta et al., 2015)

Prey location: sound reception



Ekdale & Racicot (2014)



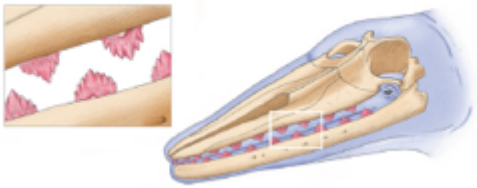
T. truncatus (C. Buell)

B. musculus (C. Buell)

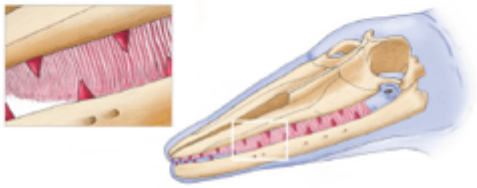
Hypotheses for teeth – baleen transition

Peredo et al., 2017

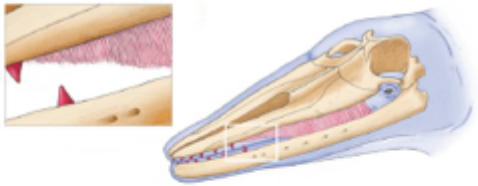
Peredo et al. , 2018



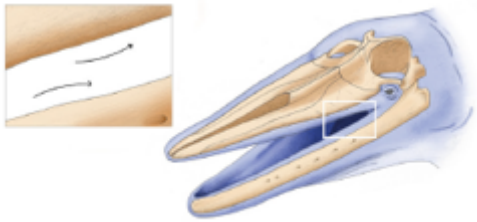
1. Dental Filtration



2. Medial Baleen

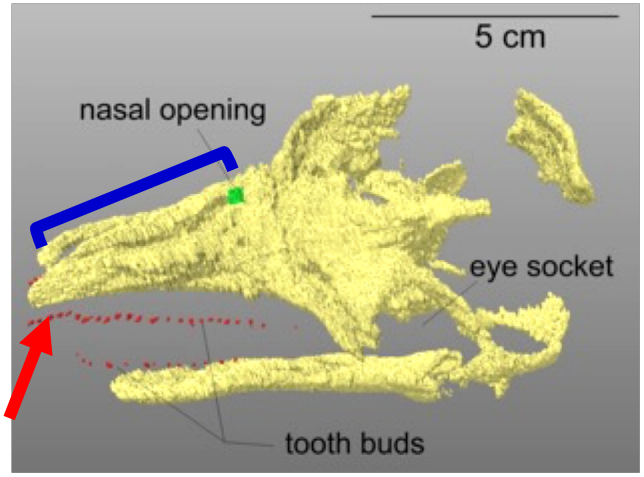


3. Posterior Baleen

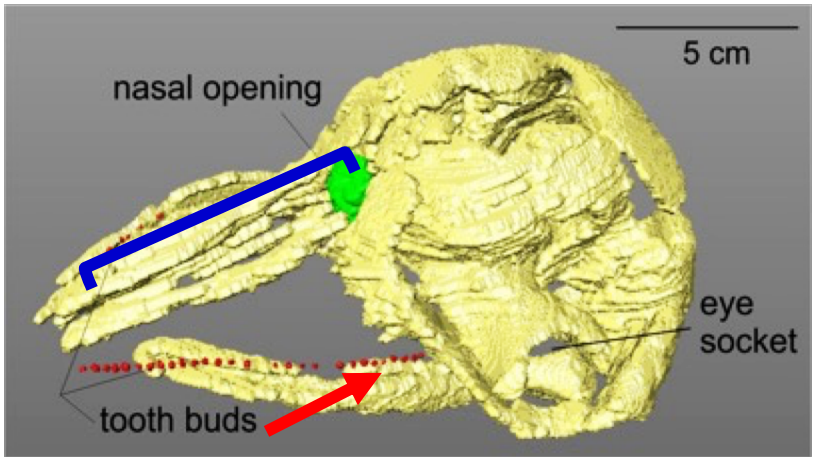


4. Suction Feeding

CT study of mysticete fetuses skull and dentition development

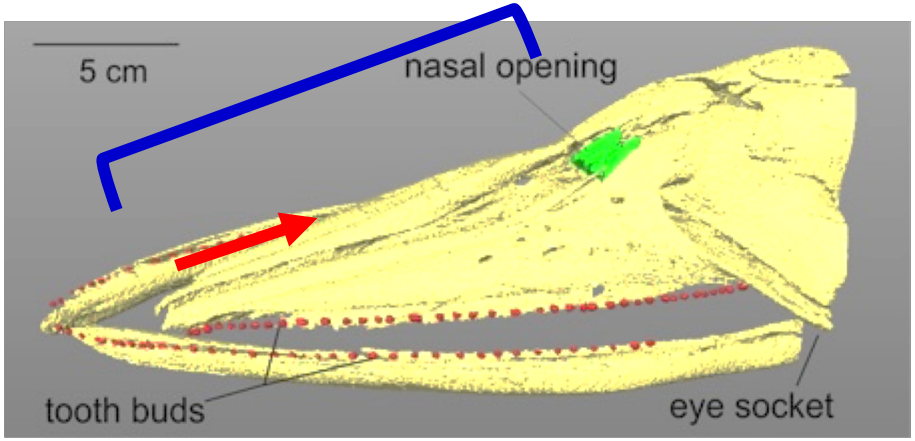


3 months old



4-5 months old

Humpback whale



6 months old

Lanzetti, Berta, Ekdale 2018