What are the limits on whale ear bone size? Non-isometric scaling of the cetacean bulla

Sabrina L Groves Corresp., [1, 2], **Carlos Mauricio Peredo** [1, 3, 4], **Nicholas D Pyenson** [1, 5]

[1] Department of Paleobiology, National Museum of Natural History, Washington D.C., District of Columbia, United States
[2] Department of Biological Sciences, Mount Holyoke College, South Hadley, MA, United States
[3] Department of Earth and Environmental Science, University of Michigan - Ann Arbor, Ann Arbor, Michigan, United States
[4] Department of Marine Biology, Texas A&M University - Galveston, Galveston, Texas, United States
[5] Department of Paleontology and Geology, Burke Museum of Natural History and Culture, Seattle, Washington, United States

Corresponding Author: Sabrina L Groves
Email address: grove23s@mtholyoke.edu

The history of cetaceans demonstrates dramatic macroevolutionary changes that have aided their transformation from terrestrial to obligate aquatic mammals. Their fossil record shows extensive anatomical modifications that facilitate life in a marine environment. To better understand the constraints on this transition, we examined the physical dimensions of the bony auditory complex, in relation to body size, for both living and extinct cetaceans. We compared the dimensions of the tympanic bulla, a conch-shaped ear bone unique to cetaceans, with bizygomatic width—a proxy for cetacean body size. Our results demonstrate that cetacean ears scale non-isometrically with body size, with about 70% of variation explained by increases in bizygomatic width. Our results, which encompass the breadth of the whale fossil record, size diversity, and taxonomic distribution, suggest that functional auditory capacity is constrained by congruent factors related to cranial morphology, as opposed to allometrically scaling with body size.

What are the limits on whale ear bone size? Non-isometric scaling of the cetacean bulla

Sabrina L. Groves[1,2*], Carlos Mauricio Peredo[1,3,4], Nicholas D. Pyenson[1,5]

[1]Department of Paleobiology, National Museum of Natural History, Washington D.C.
[2]Department of Biological Sciences, Mount Holyoke College, South Hadley, Massachusetts
[3]Department of Earth and Environmental Science, University of Michigan - Ann Arbor, Ann Arbor, Michigan
[4]Department of Marine Biology, Texas A&M University - Galveston, Galveston, Texas
[5]Department of Paleontology and Geology, Burke Museum of Natural History and Culture, Seattle, Washington

[*]Corresponding Author:
S.L. Groves
grove23s@mtholyoke.edu

Abstract

The history of cetaceans demonstrates dramatic macroevolutionary changes that have aided their transformation from terrestrial to obligate aquatic mammals. Their fossil record shows extensive anatomical modifications that facilitate life in a marine environment. To better understand the constraints on this transition, we examined the physical dimensions of the bony auditory complex, in relation to body size, for both living and extinct cetaceans. We compared the dimensions of the tympanic bulla, a conch-shaped ear bone unique to cetaceans, with bizygomatic width—a proxy for cetacean body size. Our results demonstrate that cetacean ears scale non-isometrically with body size, with about 70% of variation explained by increases in bizygomatic width. Our results, which encompass the breadth of the whale fossil record, size diversity, and taxonomic distribution, suggest that functional auditory capacity is constrained by congruent factors related to cranial morphology, as opposed to allometrically scaling with body size.

Introduction

The evolutionary history of cetaceans exhibits dramatic transformations that have facilitated their ecological transition from a terrestrial to an obligate marine lifestyle (Pyenson, 2017; Zimmer, 2011). The cetacean fossil record shows extensive anatomical modifications that allowed for this transition by facilitating communication and navigation underwater. This adaptation to life in the water, from terrestrial ancestry, required surmounting or accommodating physical constraints to the functional challenges for hearing (Nummela et al. 2007; Ketten, 1994). Previous studies have documented allometric patterns associated with precocial growth in the ear bones (i.e., tympanoperiotic complex) of living cetaceans, demonstrating that extant cetacean ontogeny is, at least partially, driven by acoustic ecology (Lancaster, 2015; Yamato and Pyenson, 2015; Ekdale, 2015; Thean et al., 2017). This study seeks to understand the allometry of cetacean ear bones across their evolutionary history to elucidate the extent to which acoustic ecology constrains variability in tympanic bulla morphology.

The cetacean auditory system has undergone dramatic modifications associated with at least three major shifts throughout cetacean evolutionary history: (1) the land-to-sea transition; (2) ultrasonic hearing for echolocation; and (3) infrasonic hearing in mysticetes (Thean, 2017; Thewissen & Williams, 2002; Spoor et al. 2008; Thewissen et al. 2001; Fleischer, 1976; Schevill, 1953). Throughout these changes, cetaceans have maintained a unique auditory structure: the pachyosteoslerotic tympanic bulla. The tympanic bulla's large, dense, conch-shaped structure works with the mandibles and soft tissues of the inner ear (e.g., inside the periotic) to detect and isolate sound (Luo and Gingerich, 1999; Cozzi et al. 2015; McCormick et al. 1970). The bulla combines with the periotic to form the tympanoperiotic complex (Mead & Fordyce, 2009). The tympanoperiotic complex is highly diagnostic for taxonomic and phylogenetic research (Ekdale et al. 2011, 2015), and it is readily preserved in the fossil record, providing a marker of acoustic evolution (Churchill et al., 2016; Park et al., 2016, 2019; Mourlam & Orliac, 2017; Racicot et al. 2018, 2019). Thus, this anatomical unit is useful for studying allometric patterns in cetacean evolutionary history.

Here, we use a comparative dataset of cetacean tympanic bullae, generated from museum specimens and the published literature, spanning the full range of cetacean body size, to test the extent to which body size drives tympanic bulla size. Previous work has shown that some inner ear structures (specifically the bony labyrinth) are strongly correlated with body mass (Ekdale 2015; Racicot et al. 2016). However, biological systems rarely scale isometrically, and modern whales are seemingly approaching an upper limit on body size (Slater et al. 2017; Goldbogen et al. 2019; Gearty et al. 2018), suggesting osteological and/or ecological constraints on scaling. Our study demonstrates that bullae become proportionally smaller as body size increases. Thedataset relies on accessible, low-cost measurement techniques, and includes fossils spanning all of cetacean evolutionary history, including the earliest semi-aquatic stem cetaceans, and major ecological transitions (Pyenson, 2017). We demonstrate that the scaling of tympanic bullae is positively allometric, non-isometric, and smaller than anticipated at the largest body sizes.

Materials & Methods

Anatomical Measurements

We measured the bizygomatic width (BZW), tympanic bulla length (BL), and tympanic bulla width (BW) of cetacean skulls using handheld calipers ($\pm$ 1mm). Bizygomatic width was defined as the maximum distance between the lateral edges of the zygomatic processes and was used as a proxy for cetacean body size (Pyenson & Sponberg 2011). In the case of incomplete skulls, the bizygomatic width was measured from the lateral edge of one zygomatic process to the midline and doubled. BL was measured in the dorsal and lateral views from the outer posterior prominence to the edge of the involucral ridge following previous authors and as documented by Tsai & Fordyce (2015) and references therein. Bulla width was measured in ventral views from the mallear ridge to the involucrum following Tsai & Fordyce 2015 and Tanaka et al. 2018 (Fig. 1). Where possible, we measured both the right and left bulla and used the mean value in this study. Only complete and intact specimens were included in the final dataset. Other studies have used the periotic, specifically inner ear structures such as the spiral cochlea and the bony labyrinth, to test for changes in acoustic ecology through whale evolutionary history. Here, we elect to focus on the tympanic bulla because it is an external structure that can be measured with minimal resource allocations and because tympanic bullae preserve readily in the fossil record, making it easier to amass a large dataset that can be easily replicated.

Figure 1. 3D models of sample cetacean skulls illustrating the measurements collected for this study, including (A) a stem cetacean (*Zygorhiza*, USNM PAL 11962), (B) a mysticete (*Balaenoptera*, USNM VZ 593554), and (C) an odontocete (*Tursiops* USNM VZ 550969). Specimens are scaled to the same condylobasal length. BZW: Bizygomatic width, measured as the maximum distance across the zygomatic processes of the squamosals or estimated by doubling the measurement to the midline. BL: tympanic bulla length measured along its longest anteroposterior axis following the orientation guidelines of Mead and Fordyce (2009). BW: tympanic bulla width measured along its widest transverse axis following the orientation guidelines of Mead and Fordyce (2009).

Institutional Abbreviations

UMMP

University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA.

USNM

Departments of Paleobiology and Vertebrate Zoology (Division of Mammals), National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA.

Data Acquisition and Taxonomic Selection

We measured the bizygomatic width, bulla length, and bulla width for specimens that preserve both skulls and at least one complete tympanic bulla. Our data set includes fossil cetaceans from the UMMP and USNM; we then supplemented this dataset with additional measurements from published specimens from the literature. Juvenile and subadult specimens were excluded as examining ontogenetic growth is beyond the scope of this study. The final dataset (Table S1) includes 267 representatives of nearly every known cetacean taxon (n=135) with pairable bizygomatic widths and tympanic bulla.

Phylogenetic Analysis

To test for potential phylogenetic signal, we constructed a composite tree using previously established phylogenetic relationships and their heuristic searches with accepted support values (Lambert et al., 2017; Tanka & Fordyce, 2017; Marx & Fordyce, 2015; Peredo & Uhen, 2016;

Gatesy et al. 2012; O'Leary, 2001). The composite matrix, constructed in MESQUITE 3.6 (Maddison & Maddison, 2018), included three new continuous characters: BZW, BL, and BW. Phylogenetic Independent Contrasts (PICs) correlated continuous size variable traits with corresponding taxa using non-transformed data in PDTREE. Branch lengths were set to 1.0 and colors were allocated by character value (Pyenson et al. 2013). PIC axes were set as follows: Y- the character for exploration (|BL:BZW|) and X- the tree character ($\sqrt{\Sigma\rho(X,Y)}$, the square root of the sum of the correlated branch lengths). To assess the phylogenetic underpinnings of non-isometric scaling relationships, we regressed the PICs of the continuous character traits and mapped them back onto the original composite tree (Garland & Ives, 2000; Pyenson et al, 2013). The dataset exhibited a normal distribution and character trait ranges were spread across families.

Results

Allometry of Cetacean Tympanic Bullae

Scaling relationships of tympanic bulla length (Fig. 2A slope= 0.5488x, R^2= 0.7055) and bulla width (Fig. 2B slope= 0.5644x, R^2= 0.6824) versus bizygomatic width were positively allometric (Fig. 2). This trend suggests that body size is the predominant correlate influencing ear size, with roughly 70% of the bullae dimensional variation being explained by changes in body size. We used log-transformed plots to display linear regressions across the sample, allowing size extremes to be shown with minimal axis compression (Fig. 2). The smallest cetaceans (e.g., *Cephalorhynchus hectori*, *Pontoporia blainvillei*, and *Phocoena phocoena*) had bullae that were about twice as long as they were wide (BL:BW 1.7-2.2). Conversely, the largest cetaceans (e.g., *Eubalaena glacialis, Megaptera novaeangliae*, *Balaenoptera physalus*) exhibited bullae nearly as wide as they were long (BL:BW 1.1-1.7). At smaller body sizes (BZW<185mm), the tympanic bulla length was consistently 15–41% of bizygomatic width. However, at larger body sizes (BZW>407mm) bulla length was closer to 10% and as low as 4% of bizygomatic width in some specimens of *Megaptera novaeangliae* and *Balaenoptera physalus*, indicating that tympanic bullae are proportionally smaller at the largest body sizes.

Figure 2. Log-transformed bivariate plot demonstrating allometric changes in bulla size and bizygomatic width: **A.** Tympanic bulla length versus bizygomatic width. **B.** Tympanic bulla width versus bizygomatic width. Black dots represent specimens from the amalgamate dataset. Colored lines represent linear regressions. See text for statistical results.

The patterns observed in the cumulative dataset remain consistent within taxonomic groupings (stem cetaceans, odontocetes, and mysticetes). Larger body sizes were correlated with longer tympanic bulla in all three groups (Fig. 3): stem cetaceans (slope= 0.1626x, R^2= 0.7166), mysticetes (slope=0.0248x, R^2= 0.4635), and odontocetes (slope= 0.049x, R^2= 0.5868). Similar patterns were observed for body size and tympanic bulla width in stem cetaceans (slope= 0.0034x, R^2= 0.7719), mysticetes (slope= 0.0217x, R^2= 0.4100), and odontocetes (slope= 0.04x, R^2= 0.5293).

Figure 3. Allometric relationships of stem cetaceans, odontocetes, and mysticetes: **A.** Tympanic bulla length (BL) versus bizygomatic width (BZW). **B.** Tympanic bulla width (BW) versus bizygomatic width (BZW). Green circles represent stem cetaceans, red correspond with odontocetes, and blue indicate mysticetes. Colored lines represent linear regressions by group.

Within groups, our data demonstrated insignificant linear growth trajectories, with stem cetaceans and odontocetes constrained to the left side of the graph likely as a result of their smaller body sizes, and mysticetes occupying a wide range of ear and body sizes (Fig. 2-3). As a paraphyletic group, stem cetaceans resemble the tympanic bullae size and proportions of odontocetes despite larger body sizes comparable to those of smaller mysticetes (Fig. 3). The composite dataset includes a diverse assortment of bulla and bizygomatic sizes.

Tympanic bullae and bizygomatic width seemingly conform to the same scaling coefficient, regardless of taxonomic grouping (Fig. 2, 3). Our phylogenetic independent contrasts (PIC) yielded no genus-level clustering in both branch proximity and corresponding character traits, indicating that tympanic bulla size is not governed by phylogeny (Fig. S1).

Discussion

Scaling & Function

Tympanic bullae play a fundamental role in cetaceans' abilities to navigate, communicate, and feed within aquatic systems. Our results demonstrate that cetacean bulla dimensions increase in a positively allometric pattern irrespective of taxonomic identity or phylogenetic history. Nonetheless, the largest cetaceans (mysticetes) exhibit disproportionately small tympanic bullae, while small-bodied cetaceans (e.g. *Pontoporia, Platanista*, phocoenids, and extinct odontocetes such as *Olympicetus* and *Echovenator*) exhibit particularly large ears for their body sizes (Fig. 3). These small-bodied odontocetes all retain proportionately large tympanoperiotic complexes, possibly hinting at a lower limit for cetacean bulla size. Notably, the largest cetaceans are all extant (Rosel et al. 2020; Pyenson & Sponberg, 2011; Vermeij & Pyenson, 2016; Slater et al., 2017). Whale body size persists near a lower bound for much of their evolutionary history and only reached extreme gigantism during the Plio-Pleistocene (Slater et al. 2017). Such departures from linearity suggest that functional auditory capacity is not based on proportional congruences, but may instead be constrained by functional or biological auditory limits.

One such constraint may be osteological: the tympanic bulla functions by acoustically isolating the hearing apparatus from the rest of the skull (Luo and Gingerich, 1999; Nummela et al. 2004; Cozzi et al. 2015) and it remains unclear how acoustic isolation functions at proportionally larger body sizes. Another potential limitation may be ecological. The pachyosteosclerotic bulla enhances the reception of sound underwater, and may therefore be bound within a functional size range with upper and/or lower limits of effectiveness. This constraint is likely true for echolocating odontocetes, which rely on high frequency sounds not just for communication, but for navigation and feeding as well (Ketten, 1994). Future research is needed to determine how bulla size influences sound reception underwater. Finally, cetaceans often exhibit paedomorphic ear bone morphology at birth (Cozzi et al. 2015; Yamato and Pyenson, 2015), suggesting that future work examining changes in allometry across whale ontogeny may reveal developmental constraints on ear bone scaling. Such studies would necessarily focus on extant sampling, as developmental series are mostly lacking from the fossil record of cetaceans.

Evolutionary Patterns

Cetaceans underwent major morphological transformations associated with an increasingly marine lifestyle, but our results demonstrate that tympanic bulla allometry remains relatively unchanged throughout 50 million years of cetacean evolutionary history. Stem cetaceans maintain a stronger consistent relationship between tympanic bulla dimensions and body size than either of the crown groups (Fig. 3). This pattern may hold because stem cetaceans exhibit small and medium body sizes overall, but generally not the gigantism observed in extant mysticetes (Fig. 3). Despite innovations that involve hearing, such as ultrasonic echolocation in odontocetes and extreme gigantism in mysticetes, neither extant lineage differs markedly from stem cetaceans in terms of tympanic bullae dimensions and scaling. This result is noteworthy given their seemingly disparate ecologies and suggests little functional selection on tympanic bulla dimensions. Instead, bulla dimensions converge around a common form. The consistency of tympanic bulla dimensions across the land-to-sea transition, even in stem cetaceans, reinforces the hypothesis that even the earliest cetaceans already had aquatic-adapted tympanic bullae (Luo and Gingerich, 1999; Nummela et al. 2004).

Notably, while our study examines the relationship between tympanic bullae size and body size, it does not directly test whether changes in tympanic bulla size are driven by ecological factors. Future studies might test specific ecological factors as potential drivers of bulla size to help elucidate the relationship between ear size and functional ecology. For example, it remains unclear whether bullae can reach substantially larger sizes, or if the observed values in extant whales represent an upper limit, as seems to be the case for body size (Slater et al. 2017). Further study in this regard will reveal to what extent tympanic bulla size and shape are restrained by functional ecology. Recent authors have begun to elucidate the specific mechanism for infrasonic hearing in mysticetes (Park et al 2017, Ekdale et al. 2015), though it remains overall less understood than ultrasonic hearing in odontocetes. Consequently, future work in this area has the potential to inform a potential relationship between mysticete hearing and mysticete gigantism.

Acknowledgements

We thank David Bohaska, for access to USNM paleobiology specimens, John Ososky and Michael McGowen and for providing access to USNM zoology specimens, and Adam Rountrey for access to UMMP paleobiology and vertebrate zoology specimens. We also thank Sirpa Nummela, an anonymous reviewer, and editor J. G. M. Thewissen for their thoughtful comments on the manuscript.

Funding

CMP and NDP were supported by the Remington Kellogg Fund and the Basis Foundation. CMP is further supported by National Science Foundation Award #1906181 and by the University of Michigan Society of Fellows. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Conflict of Interest

The authors declare they have no conflicts of interest.

Author contributions

Sabrina L. Groves, Carlos Mauricio Peredo, and Nicholas D. Pyenson conceived and designed the study, performed measurements, analyzed the data, prepared figures and/or tables, and authored or reviewed drafts of the manuscript.

References

Churchill M, Martinez-Caceres M, de Muizon C, Mnieckowski J, Geisler JH (2016) The origin of high-frequency hearing in whales. *Current Biology* **26,** 2144-2149.

Cozzi B, Podesta M, Vaccaro C, Poggi R, Mazzariol S, Huggenberger S, Zotti A (2015) Precocious ossification of the tympanoperiotic bone in fetal and newborn dolphins: an evolutionary adaptation to the aquatic environment? *The Anatomical Record* **298,** 1294-1300.

Ekdale EG, Berta A, Demere TA (2011) The comparative osteology of the petrotympanic complex (ear region) of the extant baleen whales (cetacea: mysticeti). *PLoS ONE* **6(6),** e21311.

Ekdale EG, Racicot RA (2015) Anatomical evidence for low frequency sensitivity in an archaeocete whale: comparison of the inner ear of Zygorhiza kochii with that of crown Mysticeti. *Journal of Anatomy* **226,** 22-39.

Fleischer G (1976) Hearing in extinct cetaceans as determined by cochlear structure. *Journal of Paleontology* **50,** 133-152.

Garland T, Ives AR (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* **155,** 346-364.

Gatesy J, Geisler JH, Chang J, Buell C, Berta A, Meredith RW, Springer MS, McGowen MR (2012) A phylogenetic blueprint for a modern whale. *Molecular Phylogenetics and Evolution*.

Gearty W, McClain CR, Payne JL (2017) Energetic tradeoffs control the size distribution of aquatic mammals. *Proceedings of the National Academy of Sciences of the United States of America* **115(16),** 4194-4199.

Geisler JH, Sanders AE, Luo Z (2005) A new protocetid whale (Cetacea: Archaeoceti) from the late middle Eocene of South Carolina. *American Museum Novitates* **3480,** 1-65.

Goldbogen JA, Cade, DE, Wisniewska DM, Potvin J, Segre PS, Savoca MS, Hazen EL, Czapanskiy MF, Kahane-Rapport SR, DeRuiter SL, Gero S, Tonnesen P, Gough WT, Hanson MB, Holt MM, Jensen FH, Simon M, Stimpert AK, Arranz P, Johnston DW, Nowacek DP, Parks SE, Visser F, Friedlaender AS, Tyack PL, Madsen PT, Pyenson ND (2019) Why whales are big but not bigger: Physiological drivers and ecological limits in the age of ocean giants. *Science* **366(6471),** 1367-1372.

Ketten DR (1994) Functional analyses of whale ears: adaptations for underwater hearing. *Proceedings in Underwater Acoustics* **1,** 264-270.

Lambert O, Bianucci G, de Muizon C (2017) Macroraptorial sperm whales (Cetacea, Odontoceti, Physeteroidea) from the Miocene of Peru. *Zoological Journal of the Linnean Society* **179**, 404-474.

Lancaster WC (2015) Precocial development within the tympanoperiotic complex in cetaceans. *Marine Mammal Science* **31(1),** 369-375.

Luo Z, Gingerich PD (1999) Terrestrial Mesonychia to aquatic Cetacea: transformation of the basicranium and evolution of hearing in whales. *University of Michigan, Papers on Paleontology* **31,** 1-98.

Maddison WP, Maddison DR (2018) Mesquite: a modular system for evolutionary analysis. Version 3.6.

Marx FG, Fordyce RE (2015) Baleen boom and bust: a synthesis of mysticete phylogeny, diversity, and disparity. *Royal Society Open Science* **2,** 140434.

McCormick JG, Wever EG, Palin J (1970) Sound conduction in the dolphin ear. *The Journal of the Acoustic Society of America* **48(6),** 1418-1428.

Mead JG, Fordyce RE (2009) The therian skull: a lexicon with emphasis on the odontocetes. *Smithsonian Contributions to Zoology* **627,** 1-249.

Mourlam MJ, Orliac MJ (2017) Infrasonic and ultrasonic hearing evolved after the emergence of modern whales. *Current Biology* **27,** 1776-1781.

Nummela S, Thewissen JGM, Bajpai S, Hussain ST, Kumar K (2004) Eocene evolution of whale hearing. *Nature* **430,** 776-778.

Nummela S, Thewissen JGM, Bajpai S, Hussain T, Kumar K (2007) Sound transmission in archaic and modern whales: anatomical adaptations for underwater hearing. *The Anatomical Record* **290,** 716-733.

O'Leary MA (2001) The phylogenetic position of cetaceans: further combined data analyses, comparisons with the stratigraphic record and the discussion of character optimization. *American Zoologist* **41,** 487-506.

Park T, Evans AR, Gallagher SJ, Fitzgerald EMG (2017) Low-frequency hearing preceded the evolution of giant body size and filter feeding in baleen whales. *Proceedings of the Royal Society B* **284,** 20162528.

Park T, Fitzgerald EMG, Evans AR (2016) Ultrasonic hearing and echolocation in the earliest toothed whales. *Biology Letters* **12,** 20160060.

Park T, Mennecart B, Costeur L, Grohe C, Cooper N (2019) Convergent evolution in toothed whale cochleae. *BMC Evolutionary Biology* **19(195),** 1-11.

Peredo CM, Pyenson ND, Marshall CD, Uhen MD (2018) Tooth loss precedes the origin of baleen in whales, *Current Biology* **28**, 1-9.

Peredo CM, Uhen MD (2016) A new basal chaeomysticete (Mammalia: Cetacea) from the Late Oligocene Pysht Formation of Washington, USA. *Papers in Palaeontology* **2(4),** 533-554.

Peredo CM, Uhen MD, Nelson MD (2018) A new kentriodontid (Cetacea: Odontoceti) from the early Miocene Astoria Formation and a revision of the stem delphinidan family Kentriodontidae. *Journal of Vertebrate Paleontology*, e1411357.

Pyenson ND (2017) The ecological rise of whales chronicled by the fossil record. *Current Biology* **27,** R558-R564.

Pyenson ND, Goldbogen JA, Shadwick RE (2013) Mandible allometry in extant and fossil Balaenopteridae (Cetacea: Mammalia): the largest vertebrate skeletal element and its role in rorqual lunge feeding. *Biological Journal of the Linnean Society* **108,** 586-599.

Racicot RA, Darroch SAF, Kohno N (2018) Neuroanatomy an inner ear labyrinths of the narwhal, *Monodon monoceros*, and beluga, *Delphinapterus leucas* (Cetacea: Monodontidae). *Journal of Anatomy* **233(4),** 421-439.

Racicot RA, Gearty W, Kohno N, Flynn JJ (2016) Comparative anatomy of the bony labryrinth of extant and extinct porpoises (Cetacea: Phocoenidae). *Biological Journal of the Linnean Society* **119(4),** 831-846.

Racicot RA, Boessnecker RW, Darroch SAF, Geisler JH (2019) Evidence for convergent evolution of ultrasonic hearing in toothed whales (cetacea: odontoceti). *Biology Letters* **15,**

20190083.

Ritsche IS, Fahlke JM, Wieder F, Andre H, Manke I, Hampe O (2018) Relationships of cochlear coiling shape and hearing frequencies in cetaceans, and the occurrence of infrasonic hearing in Miocene Mysticeti. *Fossil Record* **21,** 33-45.

Rosel PE, Archer FI, Baker SC, Boness, DJ, Brownell RL, Churchill M, Costa AP, Domning DP, Fordyce RE, Jefferson TA, Kinze C, Oliveira LR, Perrin WF, Wang JY, Yamada TK (2020) Society for Marine Mammalogy Committee: Taxonomy List. The Society for Marine Mammalogy.

Schevill WE, McBride AF (1953) Evidence for echolocation by cetaceans. *Deep Sea Research* **3(2),** 153-154.

Slater GJ, Goldbogen JA, Pyenson ND (2017). Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. *Proceedings of the Royal Society of Biology* **284,** 20170546.

Solis-Añorve A, González-Barbaa G, Hernández-Riverab R (2019) Description of a new toothed mysticete from the Late Oligocene of San Juan de La Costa, B.C.S., México. *Journal of South American Earth Science*s **89,** 337-346.

Spoor F, Thewissen JGM (2008) Comparative and functional anatomy of balance in aquatic mammals. *Sensory Evolution on the Threshold: Adaptations in Secondary Aquatic Vertebrates* **16**, 257-284.

Tanaka Y, Ando T, Sawamura H (2018) A new species of Middle Miocene baleen whale from the Nupinai Group, Hikatagawa Formation of Hokkaido, Japan. *PeerJ* **6,** e4934.

Thean T, Kardjilov N, Asher R (2017) Inner ear development in cetaceans. *Journal of Anatomy* **230,** 249-261.

Tsai CH, Fordyce RE (2015) The Earliest Gulp-Feeding Mysticete (Cetacea: Mysticeti) from the Oligocene of New Zealand. *Journal of Mammalian Evolution* **22(4),** 535-560.

Yamato M, Pyenson N (2015) Early development and orientation of the acoustic funnel provides insight into the evolution of sound reception pathways in Cetaceans. *PloS One* **10(3),** e0118582.

Zimmer C (2011). Evolution: the triumph of an idea. New York: HarperCollins Publishers, Inc.

Supplementary Information

Institutional Abbreviations

AGSO-CPC, Australian Geological Survey Organization, Symonston, Australia; AMP, Ashoro Museum of Paleontology, Hokkaido, Japan; BMNH, British Museum of Natural History, London, England; CCNHM, Cape Cod Museum of Natural History, Brewster, Massachusetts, United States of America; ChM-PV, The Charleston Museum, Charleston, South Carolina, United States of America; GMNH-PV, Gunma Museum of Natural History, Tomioka, Gunma, Japan; GNHM, Gamagori Natural History Museum, Gamagori, Japan; GSM, Georgia Southern Museum, Statesboro, Georgia, United States of America; GSP-UM, Geological Survey of Pakistan-University of Michigan collection, Islamabad, Pakistan; KMNH-VP, Kitakyushu Museum and Institute of Natural History, Fukuoka, Japan; LACM, Vertebrate Paleontology Collection, Natural History Museum of Los Angeles County, Los Angeles, California, United States of America; MAUL, Museo dell'Ambiente, Università di Lecce, Lecce, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MO, Montañita/Olón collection, Universidad Estatal Peninsula de Santa Elena, La Libertad, Ecuador; MSM, Museum Sønderjylland, Department Natural History and Palaeontology, Gram, Denmark; MUEcSj, Museum of Natural History, Autonomous University of Baja California Sur, La Paz, Baja California Sur, México; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marco, Lima, Peru; NHG, Natuurhistorische collectie van het Zeeuws Genootschap der Wetenschappen, Middelburg, The Netherlands; NMB, Natuurmuseum Brabant, Tilburg, The Netherlands; NMNH-P, Academician V. A. Topachevsky Paleontological Museum of the National Museum of Natural History of the National Academy of Sciences of Ukraine, Kiev, Ukraine; NMR, Natuurhistorisch Museum Rotterdam, Rotterdam, the Netherlands; NMV-P, Museum Victoria Mammalogy (Melbourne), Melbourne, Australia; OU, Geology Museum, University of Otago, Dunedin, New Zealand; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SAE, Museo Civico di Storia Naturale di Verona, Verona, Italy; SC, South Carolina State Museum, Columbia, South Carolina, United States of America; SMAC, Sapporo Museum Activity Center, Sapporo, Hokkaido, Japan; TNU, Department of Zoology, Taurida National University, Simferopol, Ukraine; UMMP, University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, United States of America; USNM, United States Smithsonian National Museum of Natural History, Washington D.C., United States of America; UWBM, Burke Museum, University of Washington, Seattle, Washington, United States of America.

Data Availability

The dataset is made available as an Excel file and provides measurements of bulla length, bulla width, and bizygomatic width.

Supplementary Figures

Supplementary Figure 1. The amalgamated phylogenetic tree used to compare stem cetaceans, mysticetes, and odontocetes for the PIC. Branches and nodes are colored by their character trait value, bulla length: bizygomatic width.

Supplemental References

Albright, LB, Sanders, AE, Geisler, JH (2018) An unexpectedly derived odontocete from the Ashley Formation (upper Rupelian) of South Carolina, U.S.A. *Journal of Vertebrate Paleontology* **38(4),** e1482555.

Bianucci, G (2005) Arimidelphis sorbinii a new small killer whale-like dolphin from the Pliocene of Marecchia River (Central eastern Italy) and a phylogenetic analysis of the Orcininae (Cetacea: Odontoceti). *Rivista Italiana di Paleontologia e Stratigrafia* **111(2),** 329-344.

Bianucci, G, Lambert, O, Post, K (2010) High concentration of long-snouted beaked whales (Genus Messapicetus) from the Miocene of Peru. *Palaeontology* **53(5),** 1077-1098.

Bianucci, G, Landini, W (2006) Killer sperm whale: a new basal physeteroid (Mammalia, Cetacea) from the Late Miocene of Italy. *Zoological Journal of the Linnaean Society* **148,** 103-131.

Bisconti, M (2005) Skull morphology and phylogenetic relationships of a new diminutive balaenid from the lower Pliocene of Belgium. *Palaeontology* **48(4),** 793-816.

Boessenecker RW, Fordyce RE (2015) A new genus and species of eomysticetid (Cetacea: Mysticeti) and a reinterpretation of 'Mauicetus' lophocephalus Marples, 1956: Transitional baleen whales from the upper Oligocene of New Zealand. *Zoological Journal of the Linnean Society* **175(3)**.

Boessenecker RW, Fordyce, RE (2014) A new eomysticetid (Mammalia: Cetacea) from the Late Oligocene of New Zealand and re-evaluation of 'Mauicetus' waitakiensis. *Papers in Palaeontology* **1(2)**.

Boessenecker RW, Fordyce, RE (2015) Anatomy, feeding ecology, and ontogeny of a transitional baleen whale: a new genus and species of Eomysticetidae (Mammalia: Cetacea) from the Oligocene of New Zealand. *PeerJ* **3,** e1129.

Bosselaers M (2010) A new fossil rorqual (Mammalia, Cetacea, Balaenopteridae) from the Early Pliocene of the North Sea, with a review of the rorqual species described by Owen and Van Beneden. *Geodiversitas* **36,** 331-363.

Churchill M, Martinez-Caceres M, de Muizon C, Mnieckowski J, Geisler JH (2016). The origin of high-frequency hearing in whales. *Current Biology* **26(16),** 2144-2149.

de Muizon C, Bianucci G, Martinez-Caceres M, Lambert O (2019) Mystacodon selenensis, the earliest known toothed mysticete (Cetacea, Mammalia) from the late Eocene of Peru: anatomy, phylogeny, and feeding adaptations. *Geodiversitas* **41(11),** 401-499.

Fitzgerald, EM (2006) A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proceedings of the Royal Society* **273,** 2955-2963.

Fordyce RE (1994) Waipatia maerewhenua, New Genus and New Species, Waipatiidae, New Family, an archaic late Oligocene dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore Jr., Proceedings of the San Diego Society of Natural History* **29,** 147-176.

Fordyce RE, Quilty PG, Daniels J (2002) Australodelphis mirus, a bizarre new toothless ziphiid-like fossil dolphin (Cetacea: Delphinidae) from the Pliocene of Vestfold Hills, East Antarctica. Antarctic Science **14(1),** 37-54.

Geisler JH, Boessenecker RW, Brown M, Beatty BL (2017) The origin of filter feeding in whales. *Current Biology* **27(13),** 2036-2042.e2.

Geisler JH, Sanders AE, Luo Z (2005) A new protocetid whale (Cetacea: Archaeoceti) from the late middle Eocene of South Carolina. *American Museum Novitates* **3480,** 1-65.

Gibson ML, Mnieckowski J, Geisler JH (2019) Tupelocetus palmeri, a new species of protocetid whale (Mammalia, Cetacea) from the middle Eocene of South Carolina. *Journal of Vertebrate Paleontology* **38(6),** e1555165.

Gingerich PD, Arif M, Clyde WC (1995) New archaeocetes (Mammalia, Cetacea) from the Middle Eocene Domanda Formation of the Sulaiman Range, Punjab (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan* **29(11),** 291-330.

Gingerich PD, Russell DE (1981) Pakicetus inachus, a new archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan* **25(11),** 235-246.

Gingerich PD, Ul-Haq M, Khan IH, Zalmout IS (2001) Eocene stratrigraphy and archaeocete whales (Mammalia, Cetacea) of Drug Lahar in the eastern Sulaiman range, Balochistan (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan* **30(11),** 269-319.

Goldin P, Startsev D (2014) Brandtocetus, a new genus of baleen whales (Cetacea, Cetotheriidae) from the late Miocene of Crimea, Ukraine. *Journal of Vertebrate Paleontology* **34(2),** 419-433.

Kellogg R (1924) Description of a new genus and species of whalebone whale from the Calvert Cliffs, Maryland. *Proceedings of the United States National Museum* **63(15),** 1-14.

Kimura T, Hasegawa Y (2019) A new species of Kentriodon (Cetacea, Odontoceti, Kentriodontidae) from the Miocene of Japan. *Journal of Vertebrate Paleontology* **39(1),** e1566739.

Lambert O (2009) A new beaked whale (Odontoceti, Ziphiidae) from the middle Miocene of Peru. Journal of Vertebrate *Paleontology* **29(3),** 910-922.

Lambert O, Bianucci G, Urbina M, Geisler JH (2017) A new inioid (Cetacea, Odontoceti, Delphinida) from the Miocene of Peru and the origin of modern dolphin and porpoise families. *Zoological Journal of the Linnean Society* **179(4),** 919-946.

Lambert O, de Muizon C, Bianucci G (2015) A new archaic homodont toothed cetacean (Mammalia, Cetacea, Odontoceti) from the early Miocene of Peru. *Geodiversitas* **37(1),** 79-108.

Martínez-Cáceres M, de Muizon C (2011) A new basilosaurid (Cetacea, Pelagiceti) from the Late Eocene to Early Oligocene Otuma Formation of Peru. *Comptes Rendus Palevol* **10,** 517-526.

Marx FG, Bosselaers MEJ, Louwye S (2016). A new species of Metopocetus (Cetacea, Mysticeti, Cetotheriidae) from the Late Miocene of the Netherlands. *PeerJ* **4**, e1572.

Marx FG, Kohno N (2016) A new Miocene baleen whale from the Peruvian desert. Royal Society Open Science **3(10),** 160542.

Marx FG, Lambert O, de Muizon, C (2017) A new Miocene baleen whale from Peru deciphers the dawn of cetotheriids. *Royal Society Open Science* **4,** 170560.

Marx FG, Post K, Bosselaers M, Munsterman DK (2019) A large Late Miocene cetotheriid (Cetacea, Mysticeti) from the Netherlands clarifies the status of Tranatocetidae. *PeerJ* **7,** e6426.

Marx FG, Tsai CH, Fordyce RE (2015) A new Early Oligocene toothed 'baleen' whale (Mysticeti: Aetiocetidae) from western North America: one of the oldest and the smallest. *Royal Society Open Science* **2(12)**, 150476.

Peredo C, Uhen MD, Nelson MD (2018) A new kentriodontid (Cetacea: Odontoceti) from the early Miocene Astoria Formation and a revision of the stem delphinidan family Kentriodontidae. *Journal of Vertebrate Paleontology* **38(2),** e1411357.

Peredo CM, Pyenson ND (2018) Salishicetus meadi, a new aetiocetid from the late Oligocene of Washington State and implications for feeding transitions in early mysticete evolution. *Royal Society Open Science* **5,** 172336.

Peredo CM, Uhen MD (2016) A new basal chaeomysticete (Mammalia: Cetacea) from the Late Oligocene Pysht Formation of Washington, USA. *Papers in Palaeontology* **2(4),** 533-554.

Solis-Añorve A, González-Barba G, Hernández-Rivera R (2019) Description of a new toothed mysticete from the Late Oligocene of San Juan de La Costa, B.C.S., México. *Journal of South American Earth Science* **89,** 337-346.

Steeman, ME (2009) A new baleen whale from the Late Miocene of Denmark and early mysticete hearing. Palaeontology **52(5),** 1169-1190.

Tanaka Y, Abella J, Aguirre-FernÃndez G, Gregori M, Fordyce RE (2017) A new tropical Oligocene dolphin from MontanÌƒita/OlÃ³, Santa Elena, Ecuador. *PLoS One* **12(12),** e0188380.

Tanaka Y, Ando T, Sawamura H (2018) A new species of Middle Miocene baleen whale from the Nupinai Group, Hikatagawa Formation of Hokkaido, Japan. *PeerJ* **6,** e4934.

Tanaka Y, Fordyce RE (2015) A new Oligo-Miocene dolphin from New Zealand: Otekaikea huata expands diversity of the early Platanistoidea. *Palaeontologia Electronica* **18.2.23A,** 1-71.

Tanaka Y, Fordyce RE (2016) Awamokoa tokarahi, a new basal dolphin in the Platanistoidea (late Oligocene, New Zealand). *Journal of Systematic Palaeontology* **15(5),** 365-386.

Tarasenko KK, Lopatin AV (2012) New baleen whale genera (Cetacea, Mammalia) from the miocene of the northern caucasus and ciscaucasia: 1. Kurdalagonus gen. nov. from the middle-late Sarmatian of Adygea. *Palaeontological Journal* **46(6),** 620-629.

Tsai CH, Fordyce RE (2015) The Earliest Gulp-Feeding Mysticete (Cetacea: Mysticeti) from the Oligocene of New Zealand. *Journal of Mammalian Evolution* **22,** 535-560.

Vélez-Juarbe J (2017) A new stem odontocete from the late Oligocene Pysht Formation in Washington State, U.S.A. *Journal of Vertebrate Paleontology* **37(5),** e1366916.

Figure 1

Figure 1. 3D models of sample cetacean skulls illustrating the measurements collected for this study

including (A) a stem cetacean (*Zygorhiza*, USNM PAL 11962), (B) a mysticete (*Balaenoptera*, USNM VZ 593554), and (C) an odontocete (*Tursiops* USNM VZ 550969). Specimens are scaled to the same condylobasal length. BZW: Bizygomatic width, measured as the maximum distance across the zygomatic processes of the squamosals or estimated by doubling the measurement to the midline. BL: tympanic bulla length measured along its longest anteroposterior axis following the orientation guidelines of Mead and Fordyce (2009). BW: tympanic bulla width measured along its widest transverse axis following the orientation guidelines of Mead and Fordyce (2009).

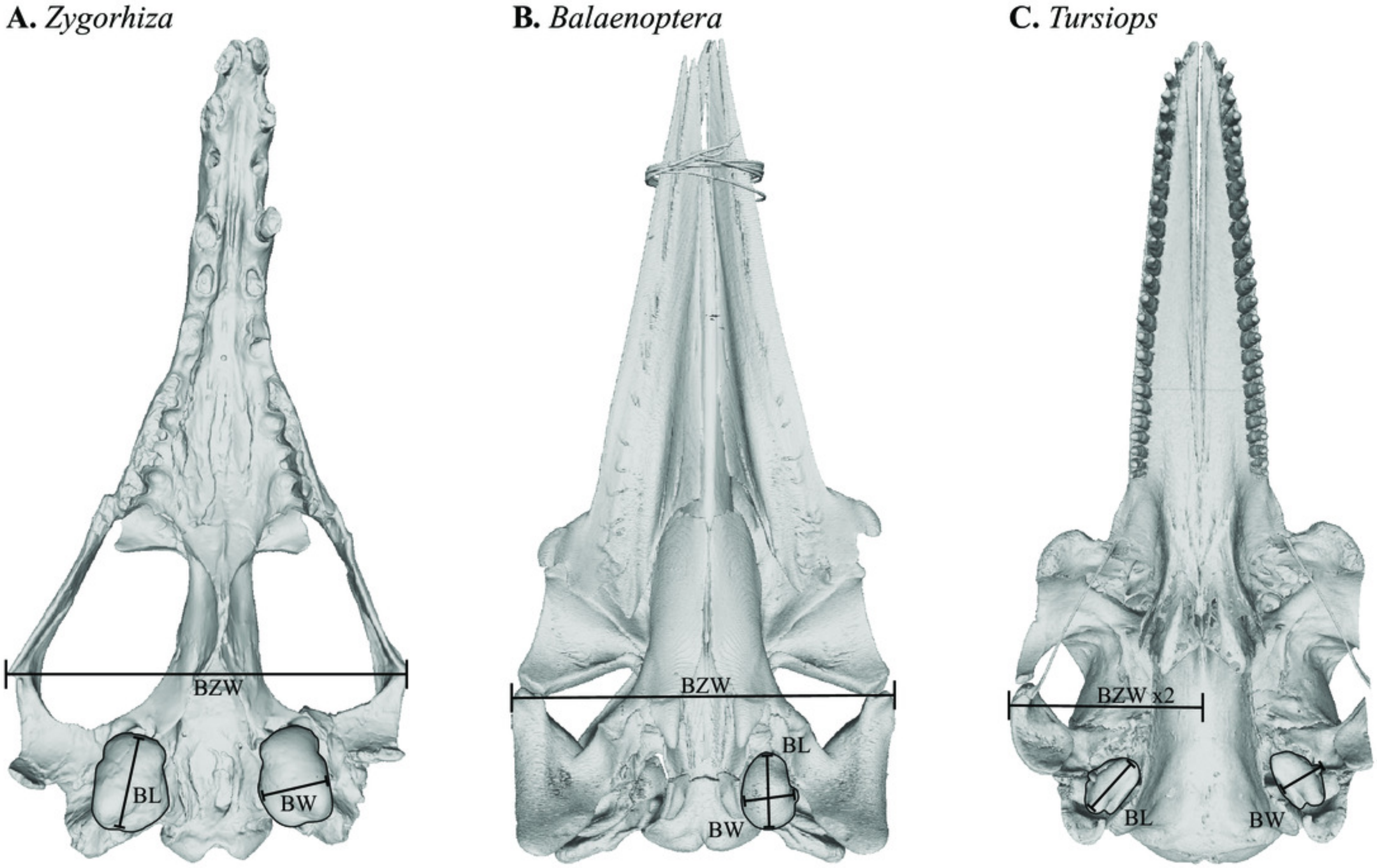
A. Zygorhiza
B. Balaenoptera
C. Tursiops
BZW
BL
BW
BZW
BL
BW
BZW x2
BL
BW

Figure 2

Figure 2. Log-transformed bivariate plot demonstrating allometric changes in bulla size and bizygomatic width:

A. Tympanic bulla length versus bizygomatic width. **B.** Tympanic bulla width versus bizygomatic width. Black dots represent specimens from the amalgamate dataset. Colored lines represent linear regressions. See text for statistical results.

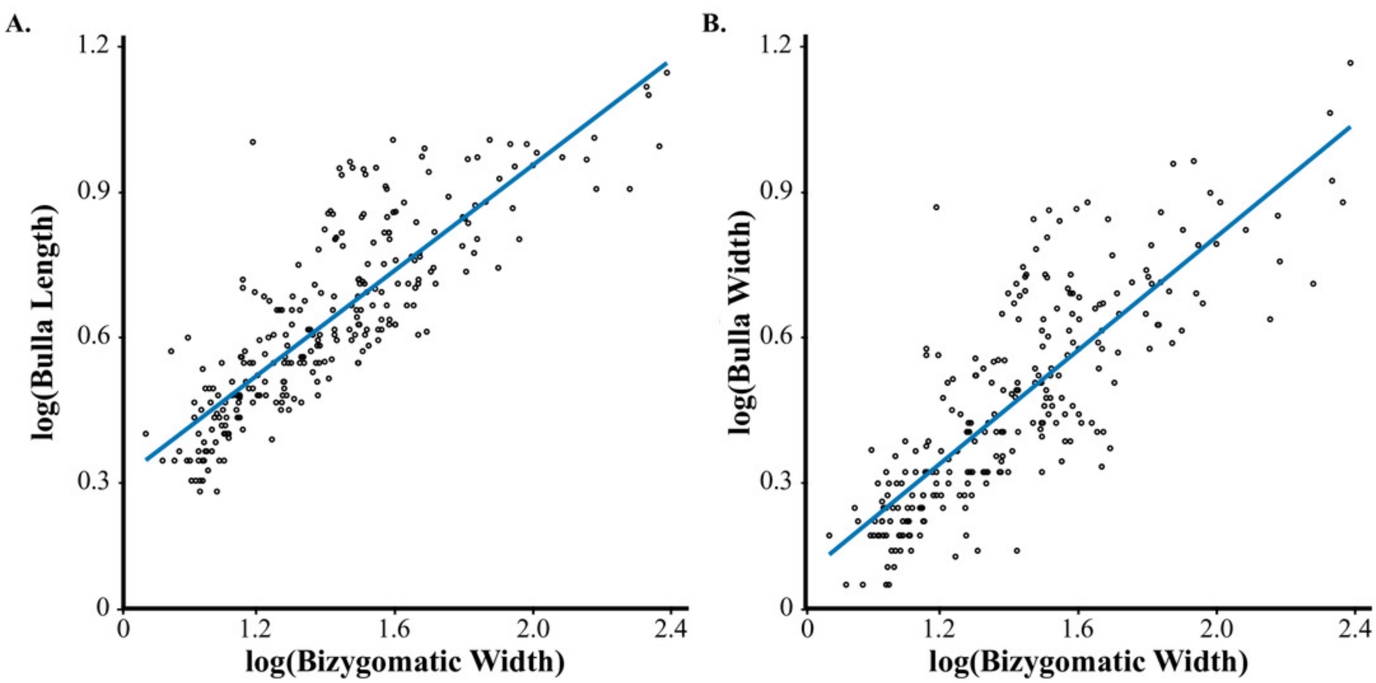

Figure 3

Figure 3. Allometric relationships of stem cetaceans, odontocetes, and mysticetes:

A. Tympanic bulla length (BL) versus bizygomatic width (BZW). **B.** Tympanic bulla width (BW) versus bizygomatic width (BZW). Green circles represent stem cetaceans, red correspond with odontocetes, and blue indicate mysticetes. Colored lines represent linear regressions by group.