



High frequency echolocation, ear morphology, and the marine–freshwater transition: A comparative study of extant and extinct toothed whales



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ABSTRACT

This study compares the bony ear morphology of freshwater and marine odontocetes (toothed whales). Odontocetes are unique among marine mammals in two important respects: 1) they use echolocation; 2) at least three lineages have independently evolved obligate freshwater habits from marine ancestries. Freshwater odontocetes include the so-called “river dolphins,” a paraphyletic group that each evolved convergent external morphological characters that distinguish them from oceanic dolphins (Delphinoidea). In addition to their convergent external morphology, “river dolphins” all have echolocation that use one peak (narrow-band) frequency around 100 kHz, compared to oceanic delphinoids which use a two peak (bimodal) frequency ranging from 40 to 140 kHz. The differences in echolocation suggest that the sensory systems responsible for detecting these different sound frequencies should also differ, although quantitative assessments of the cetacean hearing system remain understudied and taxonomically undersampled. To test if ear bone morphology reflects underlying environmentally driven differences in echolocation ability, we assembled a dataset of odontocete periotics ($n = 114$) from extant and fossil species. We examined 18 external and three internal linear periotic measurements, the latter of which were examined using cone-beam scanning tomography. Results from multivariate canonical ordination analyses show that periotic height, periotic thickness and pars cochlearis width collectively explain the largest amount of interspecific variation in our dataset. Because these particular ear bone measurements correspond to acoustic hearing ranges, we propose that they are also proxies for environmental preference (i.e., marine, freshwater and intermediate habitats) and may be useful for deciphering environmental preferences of extinct odontocetes.

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1. Introduction

Echolocation is a sophisticated biosonar system that has evolved independently in distantly related mammals (tenrecs, shrews, toothed whales, microchiropteran bats and Egyptian fruit bats; Gould, 1965; Gould et al., 1964; Au, 1993; Au et al., 2000) and several bird species (Brinkløv et al., 2013). Toothed whales (Odontoceti) are the only

mammals that have evolved this system for use underwater (Lindberg and Pyenson, 2007), where they use sound to both navigate and locate prey (Au, 1993; Au et al., 2000). To navigate underwater, odontocetes generate and transmit high-frequency sound from the forehead using a complex system of muscles, air sacs, and fat bodies, including the large, conical melon (Cranford et al., 1996; McKenna et al., 2011). Sound emitted from the forehead is then transmitted into the underwater environment, and its returning echoes are received via mandibular fat bodies, which articulate directly with acoustically isolated outer ear bones (i.e., the tympanic bullae) of the skull (Nummela et al., 2004; Cranford and Krysl, 2008). This process has been elucidated through a combination of experimental work directly with live individuals in laboratory settings (e.g., Lawrence and Schevill, 1956; Norris, 1969) and anatomical investigations on postmortem specimens (e.g., Cranford

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et al., 2008). Most in vivo experiments investigated marine dolphins (delphinoids), whereas fewer studies have looked at freshwater odontocetes (Herald et al., 1969; Pilleri, 1974).

Freshwater odontocetes are the so-called “river dolphins,” a paraphyletic grouping of four species in three lineages, one of which recently went extinct. “River dolphins” have external morphological characters that distinguish them from marine delphinoids. They include odontocete lineages that are represented by the living genera *Inia*, *Platanista*, and the recently extinct *Lipotes* (Simpson, 1945; Rice, 1998; Hamilton et al., 2001; Nikaido et al., 2001; Pyenson, 2009). *Pontoporia* is typically included among the “river dolphins,” and considered as such in this study, although it predominantly inhabits coastal to estuarine environments. On the other hand, the delphinoid species *Sotalia fluviatilis* inhabits freshwater river mouths of Amazonia, but is rarely included as a “river dolphin” because it lacks the external morphological specializations found in *Inia*, *Platanista*, *Lipotes* and *Pontoporia* (see below).

The first systematic considerations of “river dolphins” (Simpson, 1945; Kasuya, 1973) implied a single evolutionary origin for their freshwater distributions from globally distributed marine ancestors. More recent molecular (Hamilton et al., 2001; Nikaido et al., 2001; May-Collado and Agnarsson, 2006; Steeman et al., 2009) and morphological (Geisler et al., 2011) work confirms the paraphyly of this group. The revised phylogenetic arrangement, along with the biogeography of extant “river dolphins,” supports three independent invasions of freshwater habitats that are associated with a suite of convergent morphological specializations: 1) *Platanista* spp. endemic to the Indus and Ganges basins of South Asia; 2) *Lipotes*, now extinct but formerly endemic to the Yangtze River (Chang Jiang) of China; and 3) *Inia* found in the Amazon and Orinoco basins of South America (Best and da Silva, 1989; 1993).

Intriguingly, “river dolphins” display a suite of convergent morphological specializations that have been widely observed in the descriptive and systematic literature, creating confusion about the relationships of these taxa with other odontocetes. This suite of features includes many traits that diverge from the majority of delphinoids, such as flexible necks with unfused cervical vertebrae; wide, paddle-like flippers; reduced or absent dorsal fins; reduced orbits and eyes; and elongate rostra with lingual accessory cusps on the posterior dentition (Arnason and Gullberg, 1996; Cassens et al., 2000; Hamilton et al., 2001; Heyning, 1997; Rice, 1998; Simpson, 1945; Messenger and McGuire, 1998; de Muizon, 1988a, 1994). Many of these traits have also been identified in fossil odontocetes besides “river dolphins” and could be interpreted as plesiomorphic characters. For example, elongate rostra and complex posterior dentition have been identified in eurhinodelphinids and squalodontids (Fordyce, 1994). However, the molecular phylogenetic framework underpinning the paraphyly of “river dolphins” suggests that at least some of these commonalities are homoplasious adaptations to freshwater habitats.

It is not clear if the morphology underpinning sound generation and reception shows similar convergence. In terms of sound reception, the tympanic bullae and periotics of “river dolphins” have also been noted for their disparity relative to marine odontocetes (e.g., Kasuya, 1973), but detailed comparisons in a quantitative framework are lacking.

Here, we investigate one specific morphological component of sound reception by focusing on the periotic, an element that is often recovered from extant field collections during carcass preparation because it is dense, robust and relatively well protected from initial scavenging, despite being easily lost from decaying carcasses (Schäfer, 1972; Fordyce and de Muizon, 2001). These taphonomic properties also permit the periotic to be well represented in the fossil record of odontocetes (Uhen and Pyenson, 2007), and we thus incorporate data from both extant and fossil odontocetes in this dataset. Previous work (Ketten and Wartzok, 1990; Ketten, 1992) has suggested specific, linear periotic dimensions associated with acoustic signals. We selected many of these measurements, together with traditional ones (Kasuya, 1973),

and included additional new ones (Table 1) to test if external and internal periotic morphology differed between freshwater and marine odontocetes. We included fossils to test environmental assignments based on sedimentological evidence against our morphological data. In this study, we introduced fossil taxa and sedimentological data to provide important temporal and paleoenvironmental contexts that can better constrain evolutionary hypotheses about the origin of the periotic traits.

2. Materials and methods

2.1. Materials

Our dataset includes linear measurements (Table 1) from the periotics of extant and extinct odontocetes that correlate with known acoustic frequencies (see Table 2, Fig. 1). We collected a total of 18 measurements from 114 specimens that covered the following taxonomic breadth: fossil and extant Delphinidae ($n = 28$); fossil Delphinoidea indeterminate ($n = 1$); fossil and extant Iniidae ($n = 16$); fossil Inioida indeterminate ($n = 7$); fossil Kentriodontidae ($n = 24$); extant Monodontidae ($n = 1$); fossil Odobenocetopsidae ($n = 2$); extant and fossil Phocoenidae ($n = 20$); fossil Physeteridae ($n = 1$); fossil and extant Platanistidae ($n = 3$); fossil Platanistoidea ($n = 2$); and fossil and extant Pontoporiidae ($n = 9$) (see Table S1 for detailed taxonomy of less inclusive taxa).

2.1.1. Institutional abbreviations

IDSM: Instituto de Desenvolvimento Sustentavel Mamiraua, Tefe, Brazil; MACN: Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP: Museo de La Plata, La Plata, Argentina; MNHN: Museum national d'Histoire naturelle, Paris, France; MPC: Museo Paleontológico de Caldera, Atacama Region, Chile; SGO-PV: Area Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; UFSC: Laboratorio de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil; USNM: Department of Paleobiology and Division of Mammals, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A.

2.2. Methods

2.2.1. Computed volumetric tomography

We evaluated the internal cochlear morphology of the periotics (Supplementary Table 1) in our dataset using computed tomography (CT), a technology that permits high-resolution and precise imaging of small and obscured anatomical structures without modifying or destroying original voucher specimens. Specifically, in this study, we used volumetric CT with a cone beam array (I-Cat, from Imaging Science International), which provided resolution of the internal periotic morphology without gaps and with 0.2 mm precision. CT scanning with the cone beam method allowed us to scan an entire set of periotics oriented in the same plane (fixed to a wood plate with wax), thereby avoiding the effects of reflection (i.e., mirroring), and damage to the specimens. Lastly, this method produced a relative density spectrum for the specimens. The resultant DICOM images were analyzed and rendered in OsiriX (Rosset et al., 2004); we used the open polygon tool to collect all of the measurements. The measurements are described in Table 1 (see also Fig. 1).

2.2.2. Environment

To test for environmental correlations, we pre-classified the data matrix with groupings based on the observed habitat environment, as follows: riverine; fully marine; and coastal-estuarine (including the categories of coastal, shallow and epicontinental sea with freshwater input; see S1 and S2). In the case of the fossil specimens, the environmental categories were defined compiling locality, horizon, geologic

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