



Research

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Palaeontology

Ultrasonic hearing and echolocation in the earliest toothed whales

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The evolution of biosonar (production of high-frequency sound and reception of its echo) was a key innovation of toothed whales and dolphins (Odontoceti) that facilitated phylogenetic diversification and rise to ecological predominance. Yet exactly when high-frequency hearing first evolved in odontocete history remains a fundamental question in cetacean biology. Here, we show that archaic odontocetes had a cochlea specialized for sensing high-frequency sound, as exemplified by an Oligocene xenorophid, one of the earliest diverging stem groups. This specialization is not as extreme as that seen in the crown clade. Paired with anatomical correlates for high-frequency signal production in Xenorophidae, this is strong evidence that the most archaic toothed whales possessed a functional biosonar system, and that this signature adaptation of odontocetes was acquired at or soon after their origin.

1. Introduction

Living odontocete whales possess a complex echolocation system for sensing their prey and environment. High-frequency sounds are produced in the nasal passages, transmitted through air sinuses and the fatty melon [1]. The reflected signal reaches the inner ear through acoustic fat pads surrounding the posterior end of the mandible and middle ear [2]. The advent of echolocation is thought to be a key innovation that supported exploitation of a vast pelagic biomass—vertically migrating organisms, especially cephalopods—and explosive diversification of odontocetes [3,4]. Bony correlates of nasofacial tissues linked to ultrasonic signal production have been identified in archaic fossil odontocetes [5,6], but until now we have lacked anatomical evidence from their inner ear to test for high-frequency hearing, and verify functional echolocation [6–8]. Here, we describe the cochlear anatomy in a member of the Oligocene Xenorophidae, one of the earliest diverging odontocete clades [6,8], showing that the most archaic odontocetes could detect high-frequency sound, although probably not in the upper range of some living odontocetes and retained greater sensitivity to lower frequencies. A functional echolocation system was probably a hallmark of odontocetes from their earliest divergence.

2. Material and methods

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) specimen 534010, an isolated right petiotic (electronic supplementary material, figure S1) from the Upper Oligocene Belgrade Formation at Onslow Beach, Camp Lejeune Marine Base, Onslow County, NC, USA (see [9] for details on locality and geological context).

USNM 534010 was micro-computed tomography (microCT) scanned using a Zeiss Xradia 520Versa at the Monash University X-ray Microscopy Facility for

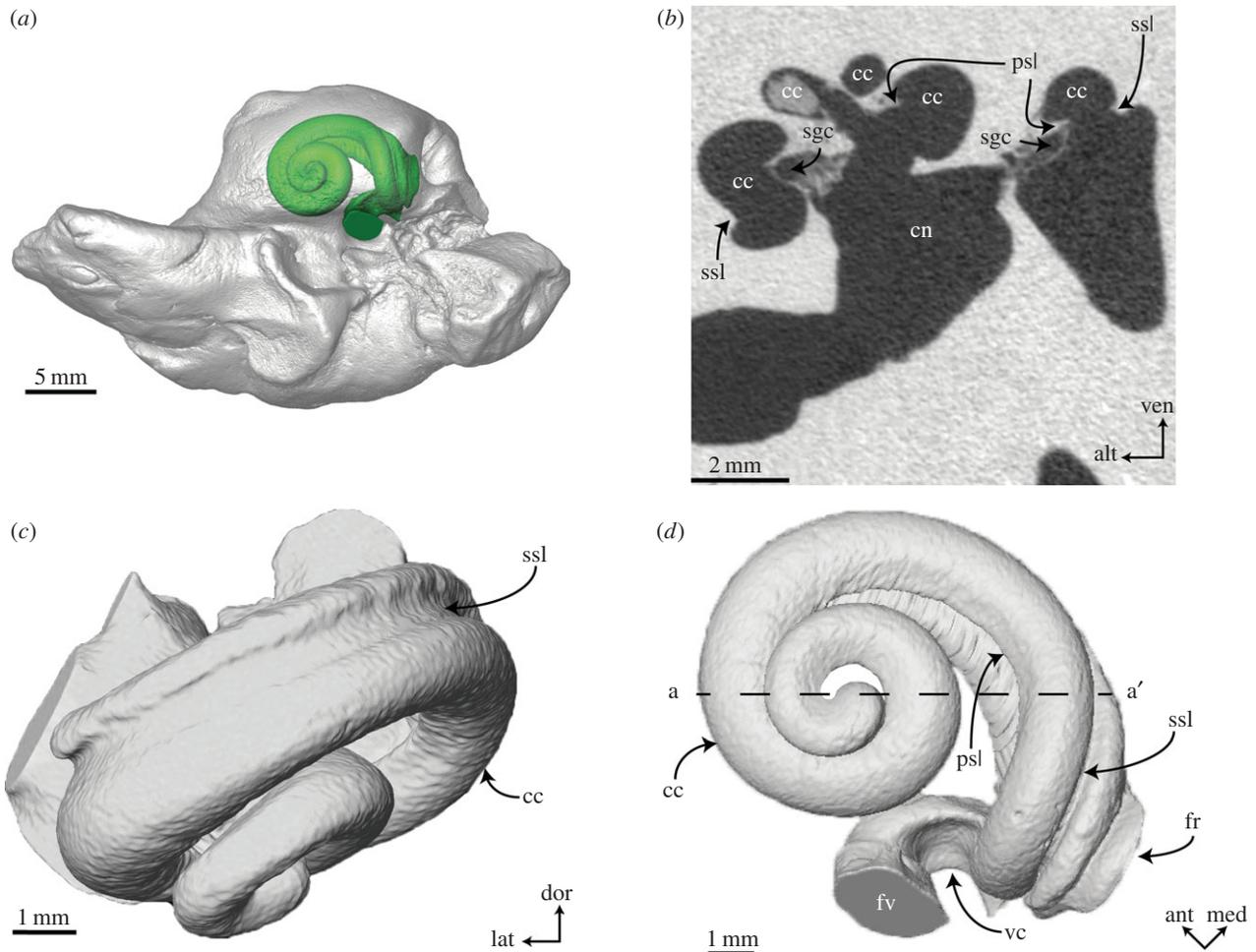


Figure 1. (a) USNM 534010, right periotic, digital model reconstructed from microCT data in ventral view. Outer surface has been made transparent to show position of the cochlea (shaded). (b) MicroCT cross-sectional slice through cochlea of USNM 534010. (c,d) Digital endocast of right cochlea of USNM 534010 reconstructed from microCT data in anterior and vestibular views. Dashed line a–a' indicates position of slice in section (b). alt, anterolateral; ant, anterior; cc, cochlear canal; cn, canal for cranial nerve VIII (auditory nerve); fr, fenestra rotunda; fv, fenestra vestibuli; med, medial; psl, primary spiral lamina; sgc, spiral ganglion canal; ssl, secondary spiral lamina; vc, vestibular curve; ven, ventral. (Online version in colour.)

Imaging Geo-materials (XMFIG). Raw data from these scans (electronic supplementary material, figure S2) were then used to create a three-dimensional model of the periotic using AVIZO (v. 8.1.0 Standard; figure 1) [10]. From this model, an endocast of the cochlea was digitally segmented using AVIZO (figure 1; electronic supplementary material, figure S3). This process was also carried out on a comparative sample of seven modern odontocete taxa and one modern mysticete taxon (electronic supplementary material, figure S4). An estimate of the low-frequency hearing limit for the xenorophid was calculated from the linear regression of low-frequency hearing limit and radii ratio for other mammals performed by Manoussaki *et al.* [11]. Detailed methods can be found in the electronic supplementary material.

3. Results

USNM 534010 possesses a combination of characters unique to the periotic of xenorophid odontocetes (electronic supplementary material, figure S1): (i) transversely thin, blade-like anterior process (apomorphic), (ii) indistinct anterior bullar facet, (iii) indistinct or absent fovea epitubaria, (iv) elongate lateral tuberosity (apomorphic) [5], (v) wide pars cochlearis with a trapezoid outline in ventral view, (vi) salient dorsal crest, (vii) dorsal crest with a dorsally concave profile in lateral view, (viii) well-developed suprameatal fossa and (ix) in

dorsal view, thick pars cochlearis medial and anterior to the internal acoustic meatus. We could not identify any potential autapomorphies of USNM 534010 shared with a particular xenorophid species (see the electronic supplementary material), hence we refer USNM 534010 to Xenorophidae, gen. et sp. indet.

The cochlea completes two turns, a number within the range of modern odontocetes [12]. The fenestra rotunda is small and is located posterior to the first quarter of the basal turn (figure 1d). This portion of the cochlea is not recurved towards the fenestra rotunda, a feature known as the 'cochlear hook', which is present in some more crownward odontocetes [13–16]. The cochlear canal retains its width for the first turn, tapering in the second turn, becoming narrowest at the apex. The cochlear aqueduct is long and sub-circular in cross section, extending dorsomedially from the basal turn just medial to the fenestra rotunda to the outer surface of the periotic.

In vestibular view (electronic supplementary material, figure S3d), the first quarter of the basal turn is more loosely coiled than the remaining 1.75 turns. The apical-most half turn slightly overlaps the basal turn. The basal ratio is 0.48, meaning that the cochlea is approximately twice as wide as it is tall. The axial pitch is 2.41 and the slope is 0.08 (table 1). The radii ratio is 5.04, a value that is slightly higher than those calculated for the modern odontocetes in

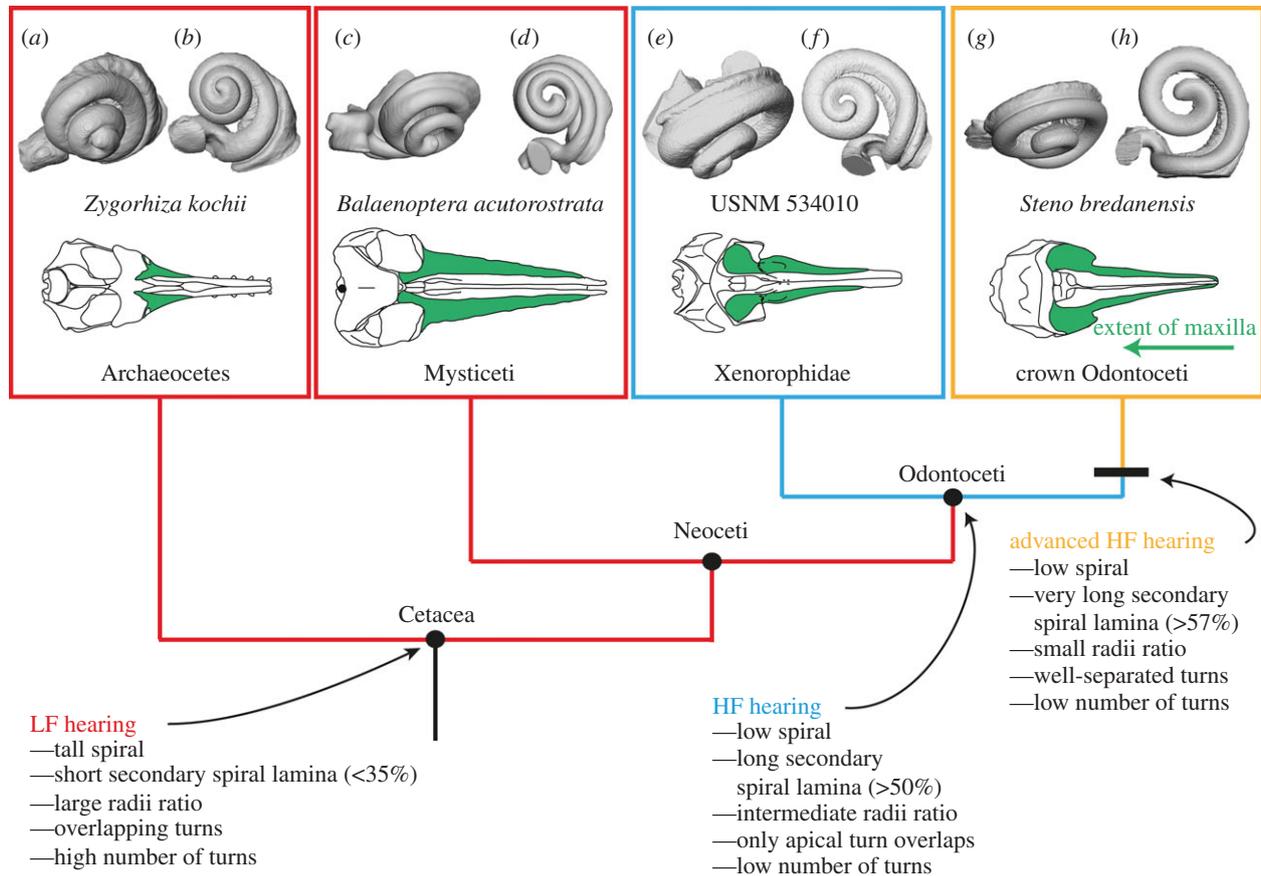


Figure 2. Evolution of odontocete hearing, based on the phylogeny of Geisler *et al.* [6], showing how the cochlea (in (a,c,e,g) anterior and (b,d,f,h) vestibular views) has become progressively more specialized towards high-frequency hearing. Line drawings of crania are in dorsal view. The line drawing representing USNM 534010 is based on *Xenorophus sloanii* and is adapted with permission from [6], © Nature Publishing Group (2014). LF, low frequency; HF, high frequency. (Online version in colour.)

Table 1. Key measurements of USNM 534010 and its estimated low-frequency limit (LFL). SSL, secondary spiral lamina.

taxon	specimen number	no. turns	canal length (mm)	radii ratio	% extent of SSL	basal ratio	axial pitch	volume (mm ³)	Estd LFL (Hz)
Xenorophidae indet.	USNM 534010	2	28.83	5.04	50	0.48	2.41	122.29	145.91

this study (except for ziphiids, values for which are unusually high for odontocetes (electronic supplementary material, table S1)). In cross section, the bone separating the basal turn from the apical turn is thick, similar to modern odontocetes (figure 1).

The primary spiral lamina extends almost the entire length of the cochlea, being widest at the base. The secondary spiral lamina extends along the radial wall of the cochlear canal for one turn (approx. 50% of the total length of the cochlear canal) (figure 1), a value slightly lower than those calculated for the modern odontocetes in this study but patently longer than for *Balaenoptera acutorostrata* (electronic supplementary material, table S1). The laminar gap is narrowest at the base. For additional comparisons, see the electronic supplementary material.

4. Discussion

Recent analyses of early odontocetes show that even the most archaic stem taxa possessed cranial morphology functionally linked to generation of high-frequency signals and therefore the

potential to echolocate [5,7,8]. The xenorophid inner ear described here corroborates the latter, demonstrating that early diverging stem odontocetes had cochleae sensitive to high-frequency sounds pivotal in echolocation. Specifically, the cochlea of USNM 534010 possesses several adaptations to high-frequency hearing: reduced number of turns, shorter cochlear length, an extended secondary spiral lamina (relative to mysticetes), a low radii ratio value and reduced overlapping of turns. These features are absent in the low-frequency-sensitive cochleae of archaeocetes and extant mysticetes [17]. The xenorophid represented by USNM 534010 would have therefore possessed a relatively stiff basilar membrane capable of detecting the echo of high-frequency sounds produced in its nasal passages.

Despite the cochlea of USNM 534010 being specialized to detect high frequencies, several features illustrate its intermediate condition relative to basilosaurid archaeocetes and crown odontocetes: an intermediate extension of the secondary spiral lamina relative to mysticetes and modern odontocetes (and therefore a less stiff basilar membrane); its radii ratio value (indicating a greater sensitivity to low-frequency sounds than crown odontocetes, with an estimated low-frequency hearing limit of 145.91 Hz, lower than any modern odontocete excepting the

aberrant ziphiids) and intermediate overlapping of turns. USNM 534010 lacks derived features seen in modern odontocetes, such as: a longer extension of the secondary spiral lamina, a small radii ratio and no overlapping turns. While xenorophids could clearly detect high-frequency sounds, they were not as specialized as modern odontocete taxa (figure 2).

At least three of the nine unambiguous synapomorphies identified for Odontoceti are nasofacial osteological correlates for echolocation [8], hinting at the importance of this sensory behaviour in the divergence and initial diversification of the clade. Thus, the ability to detect high-frequency sounds in one of the most basal odontocete lineages (Xenorophidae), as demonstrated by USNM 534010, is strong corroborating evidence that a functional echolocation system was likely present in the most recent common ancestor of xenorophids and all other odontocetes (figure 2). Within Xenorophidae, the posterior migration of the maxillae evolved independently of a convergent change in craniofacial morphology (and perhaps elaboration of high-frequency signal generation) along the stem leading to crown odontocetes [6]. This raises the possibility that there was equivalent parallel evolution towards high-frequency sensitivity in the cochleae of xenorophids and crown odontocetes. That USNM 534010 has cochlear specializations for high-frequency hearing intermediate between basilosaurid archaeocetes and crown odontocetes suggests two intriguing alternative hypotheses: (i) the 'intermediate' inner ear anatomy and degree of high-frequency sensitivity of USNM 534010 is typical for all Xenorophidae or (ii) USNM 534010 represents a basal xenorophid and hence its cochlear anatomy is plesiomorphic, while later-diverging xenorophids (like *Cotylocara*) possess cochlear

specialization for ultrasonic hearing approaching that of the crown odontocetes with which they (convergently) share an advanced state of posterior migration of rostral bones. A comparison between the cochlear canal from a *Cotylocara*-grade xenorophid and that of a more basal xenorophid is required to evaluate these hypotheses. High-frequency hearing was present in archaic odontocetes and echolocation appears to have been an important factor in their ecological and phylogenetic diversification.

Data accessibility. All additional data are in the electronic supplementary material file.

Authors' contributions. T.P. and E.M.G.F. conceived the study. T.P. and A.R.E. constructed three-dimensional models of the periotic and cochleae. E.M.G.F. photographed the specimen. A.R.E. and E.M.G.F. guided the data analysis. T.P. analysed the data. T.P., E.M.G.F. and A.R.E. wrote the manuscript. All authors approved the final draft of the manuscript. All authors agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Competing interests. We have no competing interests.

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